

Red Bunting
PART 5:

NOVEMBER, 1910.

THE
BRITISH WARBLERS
A HISTORY WITH PROBLEMS
OF
THEIR LIVES

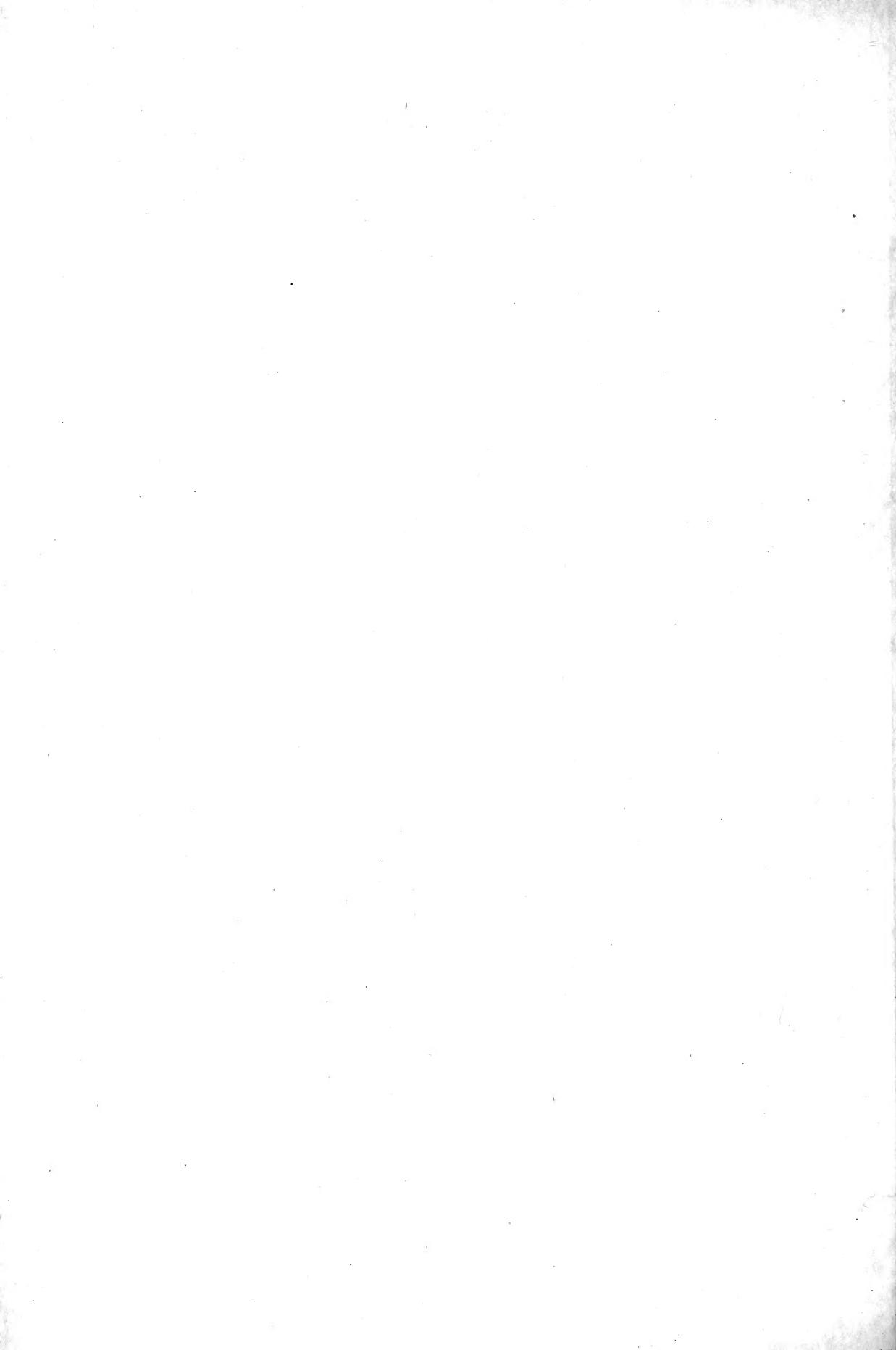
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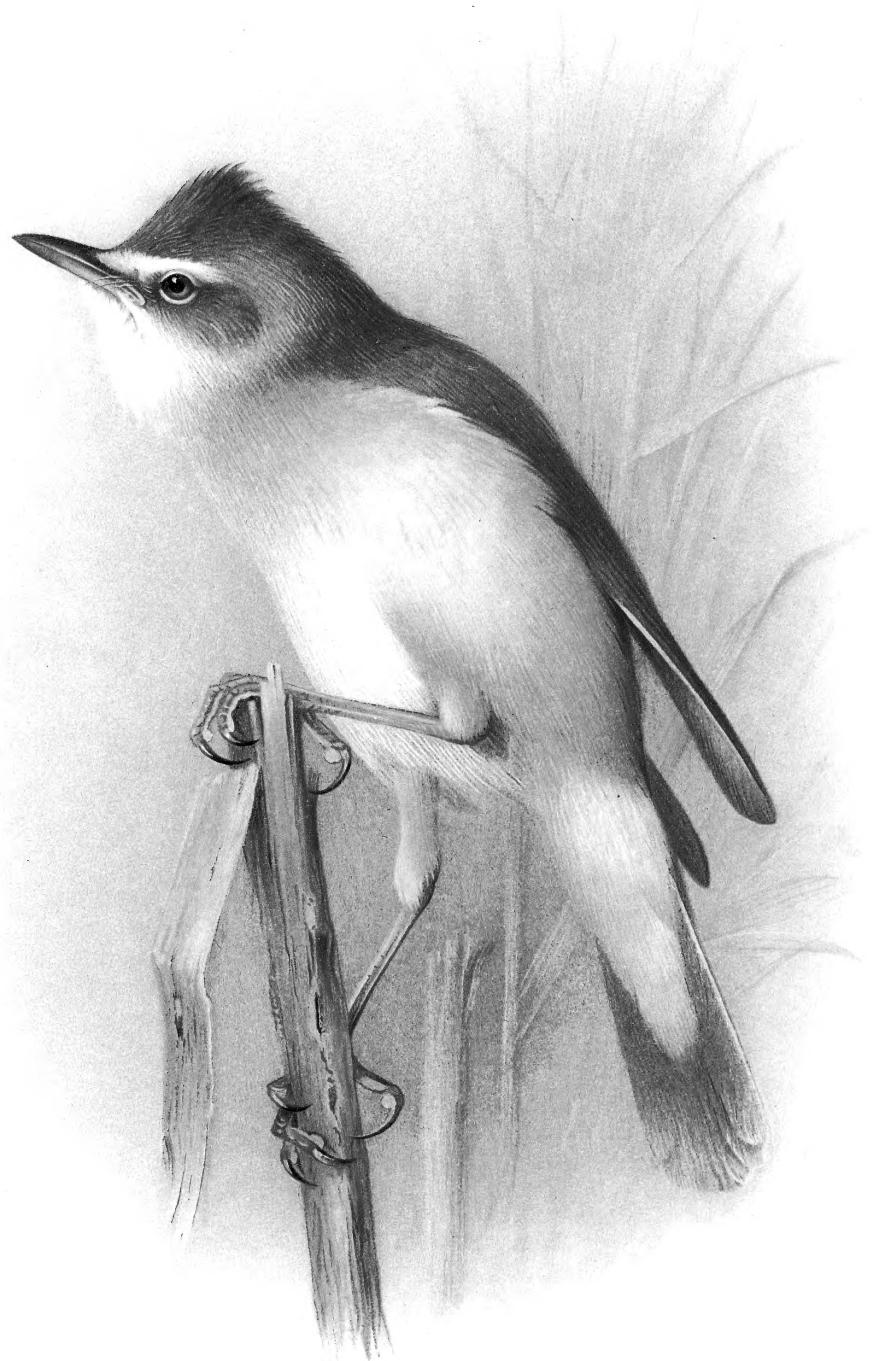
H. ELIOT HOWARD, F.Z.S., M.B.O.U.

ILLUSTRATED BY HENRIK GRÖNVOLD

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OLIVE-THROATED VIREO

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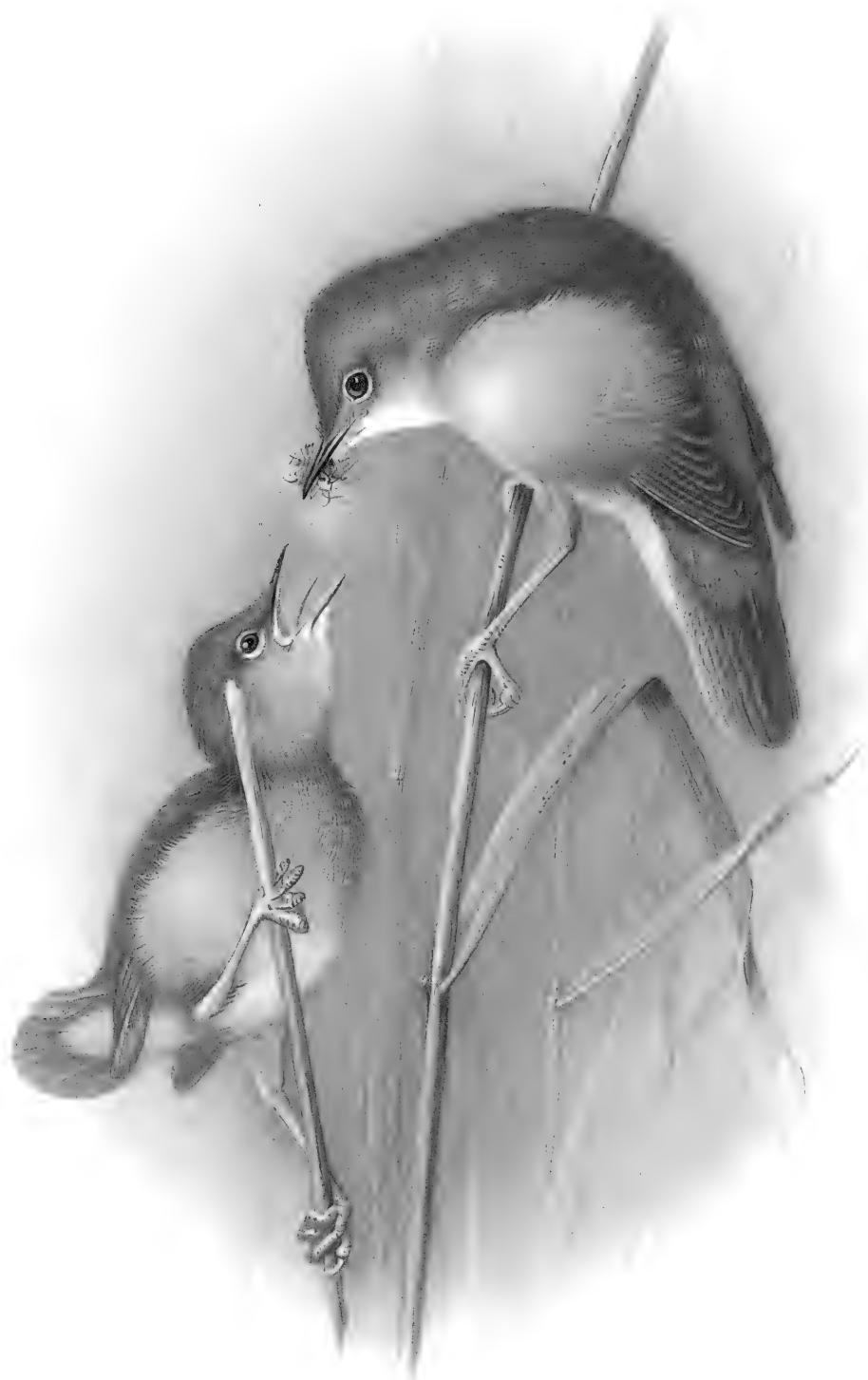
PLATES.

Reed Warbler, ad. and immature	(coloured).				
,,	variety ad. ♂	,,			
Great Reed Warbler	...	,,	♂	,,	
Melodious Warbler	...	,,	♂	,,	
Aquatic Warbler	...	,,	♂	,,	
Whitethroat ad. ♂ and	,,	♀'s (Photogravure).			
,,	,,	♂	,,
Reed Warbler	,,	♂	,,
,,	,,	♂	,,
,,	,,	♂	,,

TWO MAPS.

Showing approximate Geographical Distribution of Reed Warbler,
Marsh Warbler and Great Reed Warbler during Summer
and Winter.





REED WARBLER.

Salicaria arundinacea, *Hewitson, British Oology*, 1st Ed., vol. i, 1 p., pl. 70, fig. 1 (egg), 1834.

Sylvia arundinacea, *Meyer, British Birds*, folio Ed., vol. i. (coloured plate figuring adult and egg), 1835.

Calamoherpe arundinacea, *Macgillivray, British Birds*, vol. ii, pp. 395-396, 1839; *Gould, Birds of Great Britain*, vol. ii, 2 pp., pl. 78 (coloured figures of adults), 1862.

Salicaria phragmitis, *Hewitson, Eggs of British Birds*, 2nd Ed., vol. i, p. 87, pl. 25, fig. 2 (egg), 1846.

Salicaria strepera, *Hewitson, Eggs of British Birds*, 3rd Ed., vol. i, pp. 119-121, pl. 32, figs. 1 and 2 (eggs), 1856; *Booth, Rough Notes*, vol. ii, pp. 45-46, 1883.

Acrocephalus streperus, *Yarrell's British Birds*, 4th Ed., edited by Newton, vol. i, pp. 369-375 (woodcut), 1873; *Dresser, Birds of Europe*, pp. 567-572, vol. ii, pl. 87 (adult), 1877; *Lilford, Coloured Figures*, vol. iii, p. 36, pl. 18, (coloured figures of adult male), 1886; *Saunders, Manual of British Birds*, 2nd Ed., 79-80 (woodcut), 1897.

Acrocephalus arundinaceus, *Seeborn, British Birds*, vol. i, pp. 367-374, pl. 10, fig. 16, 1883.

Croatian, *Trstenjara parva*; Danish, *Rörsanger*; Dutch, *Kleine Karekiet*; French, *Rousserolle effarvatte*; German, *Teich-Rohrsänger*; Hungarian, *Kis Nádirigó*; Italian, *Cannajola Minore*; Swedish, *Rorsangare*; Russian, *Trotnikowaja Kamzschefka*; Spanish, *Tazaret pinzoleta*.

DESCRIPTION OF THE PLUMAGE.

Adult Male in Spring.—The upper parts generally are brownish, washed with russet, but rather more reddish brown on the rump and slightly darker on the crown. The wings and tail are brownish grey, the larger feathers being edged with the same colour as the back, though rather lighter. The lores are light brownish ash, and the sides of the head brownish grey. The throat and abdomen are white, the upper breast being suffused with a very light greyish buff, whereas the flanks are of a more russet buff and the under tail-coverts whitish buff. The underside of the tail and wings is greyish lavender, the shafts of the feathers being white. The axillaries and under wing-coverts are of a rich buff colour. The iris is dark brown and the feathers round the eye whitish. The upper mandible is blackish brown and the lower flesh colour

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though somewhat darker near the tip; mouth and tongue are orange yellow, the latter rather more red at the base, and the feet and toes lavender flesh colour.

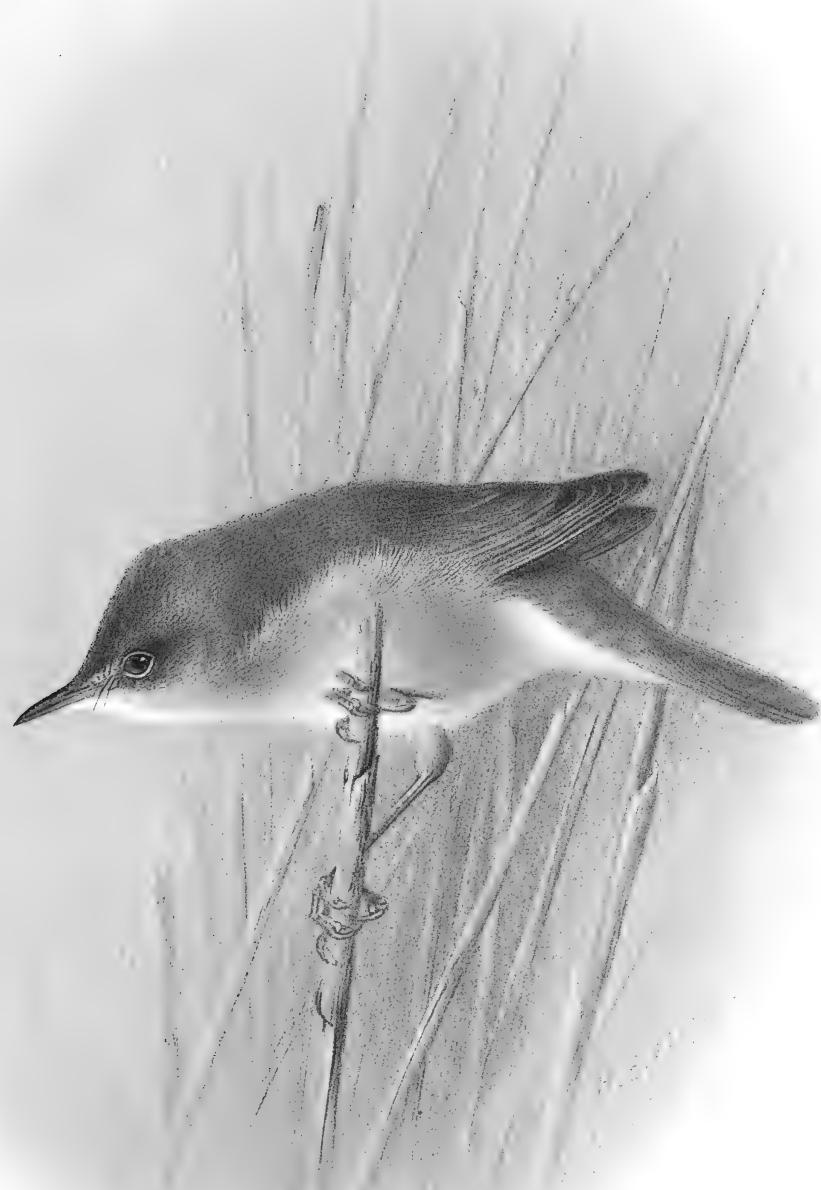
The general colour of the female is similar to that of the male.

Adult Male, light variety.—I have given a figure of this bird, which I obtained in Worcestershire, because the colouring is so similar to that of the Marsh Warbler. The colour is paler brown and less russet than the usual colour of the species, the flanks and under tail coverts being whitish buff instead of light russet buff, and the rump a slightly paler brown than the back.

Nestling.—The upper parts are rich brownish buff, wings slaty brown, the larger feathers being margined with the same colour as the back, and the throat and upper breast the same hue as the upper parts. The flanks are buff, abdomen whitish buff, under tail-coverts light buff with a slight tinge of russet, and the tail slaty brown. Iris is dark greyish brown and the eyelid slaty ash. The upper mandible is greyish lavender and the lower light lavender flesh. The colour of the mouth is similar to that of the adult. The legs are light lead colour, soles olive yellow, and claws olive grey.

GEOGRAPHICAL DISTRIBUTION.

Over the greater part of **South and Central England** it is generally distributed, but westward becomes scarce in North Devonshire, and rare in Cornwall and the **Scilly Isles**. In Derbyshire it breeds in the Trent valley only, and it is found in parts of West Lancashire and East Yorkshire, but from West and North Yorkshire, Cumberland, Westmorland and Northumberland it is absent, and from Durham there is only one record. Across the Border it is almost unknown, the only record being one from Fair Isle. In North Wales it is local and rare except on the Shropshire border, and Anglesey does not appear to be visited. In Brecknock it is fairly plentiful. There is no authenticated record of its occurrence in **Ireland**.



VARIETY



REED WARBLER

Over the greater part of **Europe** this bird is a common breeding species. In **Spain** it is found in suitable localities which are few and far between, but it breeds near the mouth of the Guadalquivir, and also in the **Balearic Islands**, while it is very common in **Portugal**, but does not nest in **Corsica** and **Sardinia**. Throughout **France**, **Belgium**, and **Holland** it is generally distributed and abundant, and the same may be said of **Denmark**, but in **Southern Sweden** we reach its northern breeding limit at Lake Wener, nearly 59° N. lat.

To **Germany** it is a common summer visitor, though less plentiful in some of the eastern provinces, and in all suitable localities in the **Austro-Hungarian Monarchy** it is numerous. In **Switzerland** we find it common and breeding even in the Alpine valleys at an altitude of 4,000 ft., and it also visits **Italy** and **Sicily** in large numbers, and is again numerous in many parts of the **Balkan Peninsula**, but has not been proved to breed in **Greece**. In **Poland** it is common, but the southern parts only of the **Baltic Provinces** are inhabited, and it is again common in the provinces of **Volhynia**, **Kiev**, **Tchernigov**, **Poltava** and **Podolia**, and occurs throughout **Southern Russia** generally, and probably also in the Crimea. From the northern slopes of the Caucasus there are no records, but on the southern slopes it has been found near Tiflis and Lenkoran, and it appears to visit Astrakhan and the Uralian Cossacks in large numbers.

There are also records of its occurrence from the **Transcaspian Province**, **Turkestan**, and the **Altai Mountains**.

In parts of **Asia Minor** it is not rare, and has bred in **Cyprus**, **Baluchistan** and **Persia**.

Of its winter quarters in **Africa** we have yet much to learn, but its range appears to be an extensive one, since it occurs as far south as **Rhodesia**, the **Orange River Colony**, and perhaps even **Cape Colony**.

It is also recorded at this season as visiting **Greece**, **Asia Minor**, **Palestine**, **Persia** and **Baluchistan**.

LIFE-HISTORY.

The home of these birds is principally among the common reed (*Arundo phragmites*), which grows in such profusion on large pools and lakes, along the banks and in the backwaters of many rivers, in canals, and in all marshy ground where there is a sufficient depth of water. And owing to the fact that reeds grow in such dense masses, the habits of this species are at all times very difficult to study. Even at the commencement of the season, before the young reeds have attained to any height, it is by no means easy to keep one individual continually in view, and if this is not done some small incident, unimportant perhaps in itself, may escape observation, without which, however, an accurate interpretation of its actions may be impossible. When the nest is built and the parents are incubating or tending their young, their habits are the more easily studied, for they are not shy nor retiring like so many species, but rapidly overcome any diffidence they may at first show when a human being is near the nest. It is even possible to cut away the reeds immediately surrounding the nest so that an uninterrupted view of their actions may be obtained, without in any way exciting their suspicions or hindering in the least a proper carrying out of their parental duties.

In the Midland counties their arrival may be expected during the first week in May; this remark refers to the forerunners of the band of migrants, which appear to be always males. The migratory movement as a whole is peculiarly erratic and somewhat difficult to understand; not that the time of advent of the first males varies very much, but that males and females intermingled continue to arrive, and to pair so long as there is sufficient territory, for some weeks after the arrival of the first male. It is sometimes suggested that the advent of the first individuals depends upon the state of growth of the reeds. Perhaps this may be true when a comparison is made between the dates of arrival in countries some distance apart, but the difference in the

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growth of the reeds from year to year in the second week of May in this country is slight, and does not appear to me to be sufficient to influence their movements. Moreover, it is not possible for a species in a foreign land to be cognisant of the state of growth of the reeds in these islands. If it can be shown that there is any relation between the two, an explanation must be sought in some peculiar climatic conditions which, while delaying the departure of the migrants, would at the same time retard the growth of the reeds. In Hungary I found these birds plentiful in the year 1905 on April 26th, and there is little doubt that they had already been there some time. On the other hand, I have no records of their arrival in this country earlier than May 1st. In the year referred to, the growth of the reeds in Hungary was undoubtedly in advance of the growth in this country. So that before we attempt to understand this question of migration, we must be in a position to decide whether, on the average, the same individuals migrate to the same country year after year. There are some grounds for believing that they do so, for it is clear that those individuals that reach Hungary about April 20th must have commenced their journey some time before those that reach this country during the first week in May.

Both males and females arrive throughout May and part of June, even as late as the 21st of the latter month. But it is by no means unlikely that some of the individuals are not "arrivals" in the sense of having only completed their journey that particular day. Indeed, it is impossible to distinguish between a male moving from pool to pool seeking territory, or similarly a female in search of a male, and a true arrival, that is to say, a bird that has only comparatively recently commenced to travel from its winter home. These later arrivals may not, therefore, be migrants in the narrower use of the term, but only individuals unsuccessful so far as reproduction is concerned. Yet it is well-nigh impossible to decide this by actual observation. Their plumage has no

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worn or ragged appearance, but the colouring is brilliant and the feathers in perfect condition, in striking contrast with those birds that have actually commenced to breed some weeks previously. The deterioration of the plumage is coincident with, if not actually the direct result of, coition, for it takes place very slowly when a bird is not breeding, but rapidly immediately reproduction has commenced. Nevertheless evidence of a much more detailed character is necessary before we can reach a final decision on this point. It even appears to be more rapid in some species than in others, being decidedly so in the case of this warbler, some individuals commencing their moult early in July. So that we find, on the one hand, members of the species arriving about June 20th in perfect plumage, and thereupon commencing to breed, and on the other, members commencing to moult early in July, having finished the task of reproduction. Thus we have what appears to be a curious irregularity, and one to which I shall refer again.

The *Arundo phragmites* is the principal but not the sole haunt of these birds, for they often frequent and build amongst the various species of *Salix* that grow along the banks of rivers, and on their way thither, or when in search of a territory, the males sometimes rest for a few days, or a few hours, in such places as osier beds, or even amongst the shrubs in gardens; but in such places they are merely sojourners, although they sing as vigorously as if they were in possession of a territory. They commence to sing on the morning after their arrival, and as they are the most persistent of singers, there is little difficulty in assuring oneself of their presence in any particular reed bed. This is especially the case before the females arrive, as they then sing almost incessantly throughout the first few hours of daylight, commencing at dawn and only lapsing into silence for short intervals. At this time of day they can often be seen perched on some horizontal reed pouring out their peculiar metallic sounding notes, or preening their feathers, their attitude at such a time being much like

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that of the Blackcap when quietly reposing, back feathers being raised, tail drooping, and breast feathers swollen out, giving them a similarly rounded appearance.

Owing to the density of the reeds, and consequently the great difficulty in studying their habits, I do not think it likely that I should ever have recognised any law of breeding territory, had I not previously known of its existence amongst so many other species, but there is little doubt that this question plays an important part in their life-history. Each male locates himself in a particular part, and a comparatively small part, of the reed bed, and inasmuch as reed beds suitable to their needs are not very plentiful, the dimensions of their territories are small. If it were not so the species would rapidly decrease, so that they differ in this respect from those migrants that inhabit many and varied situations. The males adhere more or less to a certain territory, but it is not easy to ascertain how far they struggle with one another for possession, nor whether they regard with suspicion a trespass on the part of one of their neighbours. Short but angry battles are of frequent occurrence between them for some weeks at this period. One hears the clicking of bills, and then the birds appear momentarily above the tops of the reeds, pecking at one another, and as quickly vanishing amongst the reed stems, only to reappear further away as they rapidly pursue and fight with each other. In one instance I had an exceptional opportunity of watching the behaviour of a male with regard to this question of territory. This particular bird owned a territory amongst some willows and alders adjoining a reed bed, the headquarters of his domain being a *Salix* bush overgrown with honeysuckle, and not more than fifteen yards away on the edge of the main portion of the reed bed was the territory of another pair. This latter pair must have arrived some few days before the former bird, because, when I commenced to watch the two territories on May 22nd, they were already building their nest. Morning after morning this single male behaved in much the same

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way, singing continuously while perched upon the sunny side of the bush which he had made his headquarters. If a single bird or one of another pair attempted to intrude upon his small domain, he fiercely attacked it, rapidly pursuing the trespasser some distance into the dense mass of reeds, and when a collision did occur the impact was considerable. If it was a pair that was intruding the attack was generally aimed at the male, but the female from the adjoining territory, while collecting food for her young, was also attacked. Thus the days passed by, sometimes peaceably, sometimes the reverse, until this jealous defence of his territory seemed to me to be a waste of energy and time, as it appeared to be improbable that a female would arrive at so late a date. In this, however, I was mistaken, for on June 20th a female appeared on the scene, and nesting operations were forthwith commenced. His behaviour now differed from what it had been previously; the headquarters were of secondary importance, and he now followed the female submissively. It is an interesting fact, and not a little curious, that on the day on which the female arrived—June 20th—the young of the adjoining pair finally left the nest. Why should this male for twenty-eight days have remained in the same small plot of ground? Why should he day after day have been found in the same bush and upon almost the identical branch pouring out his song? And above all, why should he have resented the approach of other members of his own species, and have attacked them so viciously? I have already mentioned this question of breeding territory in the life of other species. It is, I believe, a factor of no small importance in the animal kingdom, and as such demands further consideration.

Those who have paid attention to the habits of birds during the season in which the sexual organs are developing can hardly have failed to notice the battles which are of such frequent occurrence between the males of the same species. Darwin believed that the primary object of these struggles was the possession of a female, but for reasons

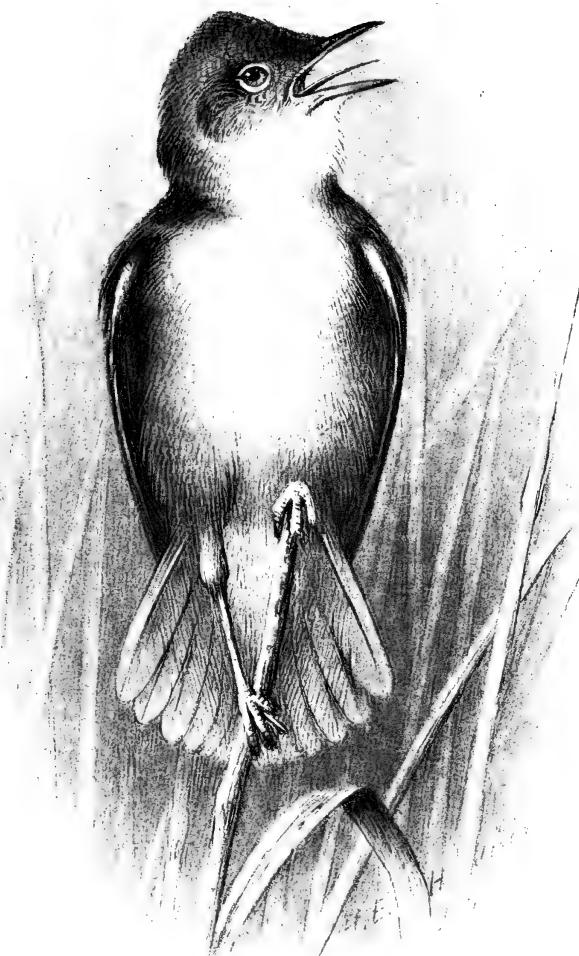
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which I shall presently give, I am inclined to think that the possession of a territory is of greater importance to the male, and is the direct cause of these struggles, which are consequently presented to us in a somewhat different light.

I well remember some years ago in the month of March being attracted by piteous cries which were proceeding from some willows that grew in an old bed of the River Severn. Quietly approaching the spot, I saw a male Blackbird (*Turdus merula*) hopping about in front of a small clump of dead vegetation, into the middle of which he was at short intervals angrily darting, and from which, as he thus darted forward, there arose the cries referred to. After watching the proceedings for a short time, I examined the dead vegetation and there found another male Blackbird crouching beneath the dead grass, in such a state of exhaustion as to be unable to stand, but only to roll from side to side, the feathers torn from its head, and traces of blood showing how severe a punishment had been administered. Raising it carefully from the ground, I removed it some distance away, hoping that it might eventually recover. Every spring the male Blackbirds can thus be seen engaged in desperate struggles. In like manner male Song Thrushes pursue and fight with one another, bunches of feathers being sometimes left upon the scene of the conflict. Male Chaffinches (*Fringilla cœlebs*) fight in mid-air and upon the ground. The males of the Coot (*Fulica atra*), and Moorhen (*Gallinula chloropus*), frequently struggle amongst themselves, the latter both upon water and land. How pugnacious the game birds become at this season is well known. I have seen one cock Pheasant pursuing another in a grass meadow for twenty minutes or more without a momentary pause. But that such small and delicate little birds as the males of the Long-tailed Tit (*Acredula caudata*) should engage in violent contests amongst themselves will scarcely be believed; nevertheless it is the case. Walking in the month of April along a country road, I noticed something fluttering a little distance ahead of me, and upon reaching the spot found two

male Long-tailed Tits engaged in a fierce conflict ; the one had seized the other by the feathers on the head, and in this way they were rolling over and over on the ground. Frightened at my approach the stronger male of the two flew away, leaving its opponent too exhausted to move. I picked it up, and while examining its head noticed the aggressor still flying round, evidently unwilling to leave. In order, therefore, to ascertain whether it would still continue the conflict in my presence, I placed its opponent again upon the ground, and retired some few paces distant, upon which the attack was renewed, and so severe was it that had I not again interfered the exhausted male must shortly have succumbed to its injuries. In the hope of saving its life I carried it some distance away and placed it in the bottom of a hedgerow. But it was then in a state of collapse, too weak even to stand, and it is doubtful whether it ultimately recovered. As in the case of the Blackbird, the principal point of attack had been the head, from which the feathers were torn in places.

Battles somewhat of this description, but with differences in detail, are of frequent occurrence at this season of the year throughout bird life in general. And since they only occur at this period, which is the period of sexual activity, it was concluded—and it must be admitted that the conclusion was not unnatural—that the females were the direct cause of the quarrels. For many reasons, principal among which was the fact that the females were seldom in evidence during the battles, this conclusion never appeared to me altogether satisfactory. The question was therefore always prominent in my mind as to what was the real meaning of these struggles, so terribly determined, and sometimes even resulting in the death of one of the combatants ; and it remained unanswered until I began to make a special study of certain migratory species. It is strange that the importance of their life-history did not impress itself upon me earlier ; for it requires but little reflection to show how splendid an opportunity is afforded in their lives for studying some of the problems with which we



MALE REED WARBLER
ATTITUDE ASSUMED DURING THE
PERIOD OF SEXUAL ACTIVITY
THE SLIGHT EXPANSION OF THE WINGS
WILL BE NOTICED.

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REED WARBLER

are confronted. It almost seems as if Nature had thus supplied us with a key to some of the mysteries of their existence. The married life of the resident species is so gradually unfolded each recurring season before our eyes, that we know not with any certainty at what point sexual development commences, and we can seldom indicate the precise moment at which that mutual attraction between the sexes occurs which ultimately leads to reproduction. But in the case of the migratory species the conditions happily are different, for since the spring migration is undertaken for the purpose of procreation, it is probable that the stimulus to that long and arduous journey is the fact that the initial stage of the development of the sexual organs has commenced. Moreover, males arrive before the females, and this fact is of immense assistance in helping us to trace out the true meaning of much of their behaviour.

I found, then, that many of those males that were the first to reach a certain district were not passing travellers only, seeking out new woods or new swamps, and leaving their places to be filled by later arrivals, but that they remained more or less in that locality in which they had settled upon their arrival ; and further observation went to show that this locality was narrowed down to a certain territory, in which the bird remained and sought its food, and which possessed definite boundaries adhered to with remarkable precision, and often, indeed, with an accuracy almost beyond belief. Furthermore I found that, when two males arrived more or less at the same time in the same locality, a battle often ensued, equally as desperate as those which occur amongst many of the resident species at this season of the year; but inasmuch as the females had not at that time arrived, it was clear that they were not the direct cause of the quarrels ; and, finally, that in the case of adjoining territories whenever a male crossed the boundary at any time during the period in which the territories were adhered to, its action was generally resented by the other male, and often led to a struggle. With

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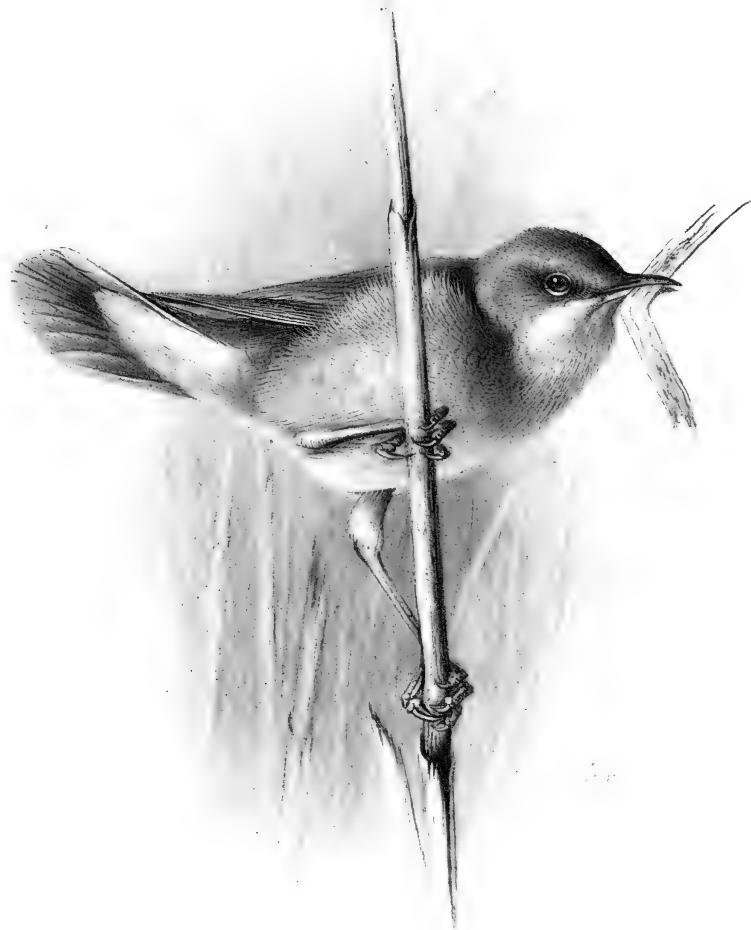
these facts before me I turned my attention again to some of those resident species whose battles had previously been a mystery. A small pool of water in front of my house afforded exceptional opportunities for studying the life of the Moorhen. This pool was inhabited by one pair, and not only was no other Moorhen allowed to approach without being attacked, but so jealous was the owner of any intrusion that he ruthlessly persecuted such harmless species as Black-birds, Starlings, and the like, when they came to the water to drink. His method of attack was as follows: he walked quietly round the edge of the water, taking advantage of every clump of rushes to conceal his approach, and when within a few feet of the intruder, raised his wings, lowered his head, and, in a threatening attitude, darted rapidly out. In connection with this particular bird I once saw an amusing incident. A covey of about twenty Partridges approached the pool, but the Moorhen from his position was only able to see the cock bird, who was leading. He therefore approached in his usual cautious manner, and when finally on the point of attacking was suddenly confronted with the remaining birds, the majority of their heads being turned in his direction. The effect was instantaneous; he assumed his normal position and retired into the rushes. On large sheets of water, inhabited by a number of pairs, a similar law as to territory will be found to prevail, each pair possessing a certain area which they regard as their own property. The habits of this bird render its life an especially suitable one for comparative study and analysis, for, of necessity, a large number are often concentrated in a small area. Therefore if some pool is kept under daily observation early in the spring, it will be found that towards the end of February, that is to say, with the rise of the sexual instinct, quarrels, sometimes developing into serious struggles, will be of frequent occurrence between different individuals. And it will be noticed that these quarrels, as a rule, have their origin in one or two individuals, or pairs, which, keeping

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respectively to certain parts of the pool, resent any intrusion thereon, and that as the days pass by, the pool, upon which formerly it was no uncommon sight to see eight or more birds in company, will be inhabited by two or three pairs only, each possessing a definite territory, and also that they still jealously guard their respective territories, resisting any intrusion on the part of their neighbours. In order to see the struggles to the best advantage, it is necessary that the pool should be kept under observation from daylight, for, strange as it may seem, the conflicts appear to be of more frequent occurrence at dawn; there are, in fact, some grounds for believing that many a battle is fought and many a territory won or lost during the hours of the night. So strongly implanted is the law of territory in this species, that a young one of not more than ten days old will attack such a bird as a Starling when settled upon the edge of the water, resembling the adults in its method of attack. Coots (*Fulica atra*) also struggle fiercely for their territories, likewise Stonechats (*Pratincola rubicola*), and the attitudes assumed by the male of the latter species when another male, or another pair, approaches its property are extravagant and often ludicrous. Both sexes of the Chaffinch are highly pugnacious at this season, and their habits are easily observed. This bird being a very common species, it often happens that some small but suitable wood is inhabited by a number of pairs and divided into adjoining territories. Early in March the males establish themselves in a certain small area, and each morning at daybreak can be heard vigorously pouring out their song. When a female arrives in one of their territories, there is considerable commotion. Sexual excitement takes the form of prolonged flights. Rising above the tops of the trees the female flies away, followed by the male, and often a considerable distance has been thus traversed before a return is made to the territory. As a consequence of this the female, more often than the male, passes the boundary, intruding upon the adjoining territory, and thus it happens

that she is sometimes attacked by the owner of that territory. But if she is followed by the male with whom she has paired, it almost always leads to a struggle. Considerable disturbance may also be caused by two pairs whose territories adjoin attacking one another. It is difficult to say with any degree of certainty what is the cause of such battles, though it sometimes seems to me possible to trace the origin to some female, recently arrived, not confining herself to the boundaries of the territory in which she has settled. But whatever it may be, the conflicts, when they do occur, are very fierce, the males and females attacking one another respectively. That Peregrine Falcons (*Falco peregrinus*) and Ravens (*Corvus corax*) will not allow another pair to breed in proximity to them is well known; and from the accounts of other observers the same law appears to be in operation in the case of the Red-necked Phalarope (*Phalaropus hyperboreus*), Waders, e.g., Ruff (*Machetes pugnax*), and the Black Grouse (*Tetrao tetrix*). I have not yet had sufficient opportunity of studying the cliff-breeding sea birds to enable me to bring forward any direct evidence from their lives, but from what I have seen little doubt remains in my mind that "acquisition of breeding territory" has exercised and is exercising a considerable influence on their life-history. How far this law extends it is impossible to say; the evidence is sufficient to show that it holds good with many species, and I shall not be surprised to learn that it is a *vera causa* of the battles so common between the males of many species of mammals and lower vertebrates.

In the life-history of the Whitethroat I have described a struggle between the females, and the attitude of the male in whose territory the battle was taking place, and I then suggested that the struggle seemed to be one of some importance to this theory. The females of some species are more brightly coloured than the males, and in such cases it is they, and not the males, that are pugnacious and fight with one another. This is so with the Phalaropes. The female Moor-



MALE REED WARBLER

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hen is more vividly coloured than the male, and it is possibly she who defends the territory, attacks all intruders, and exhibits the pugnacity referred to, although it is difficult to make certain of this, since the difference in colouring and size between the sexes is so slight that at a distance it is not very easy to distinguish them. The question we are attempting to answer is what is the cause of the battles, and whether an individual of one sex does really struggle for possession of one of the other sex. When the fighting is confined to one sex only, we might be justified, providing there were no evidence to the contrary, in assuming that the opposite sex was the immediate cause. But in the case of the Whitethroat we have a species in which the males are more brightly coloured than the females and struggle amongst themselves, but in which, contrary to expectation, the females also fight with one another. Of what advantage could it be to any species for the males to struggle for the females, and for the females to struggle for the males? This fact of the females fighting is therefore one of some importance, since it points to the existence of some other factor as the true cause of the battles. Among the large number of individuals that annually migrate together, it must sometimes happen that two females settle in the same occupied territory, and under these circumstances what could be more natural than that one should attempt to drive the other away? The ultimate object of such a battle may be said to be the male: this much I concede; but another factor is introduced by the law of territory, with the result that it matters not whether the male possesses any special attractiveness, so long as the more important consideration be fulfilled, namely, that he be the owner of a territory. The question, then, which remains to be answered is to what extent a law of battle does exist amongst the females. I mentioned at the time that in no other species had I seen the females fighting, but I have since been lucky enough to see two more instances. Both sexes of the Moorhen aid in the defence of their territory, as do both sexes of

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the Chaffinch, and, in the case of the latter species, the females struggle fiercely together, their battles being as desperate as those which occur between the males. I have seen two individuals struggling intermittently for nearly half an hour, and for the greater part of that time the fighting took place on or near to the ground. There was no doubt that the conflict was genuine; the rapid breathing, tightly drawn feathers, the rolling over and over on the ground, and the fluttering up in the air, showed this only too plainly. The male watched the contest from a branch above, and occasionally interfered by flying into the arena, but whether he attacked one bird only I was unable to ascertain; his efforts were of little avail in putting an end to the battle. This, then, is the sum-total of the evidence—insufficient, perhaps, to justify any definite conclusion; and there for the present we must leave it. But if there be any who think the evidence unreasonably scanty, supposing the struggles of the females to be a reality, I would ask them to consider this point—one to which I shall presently refer with regard to the males—that it is unnecessary for every individual to struggle for a territory, and this must be even more true of the females. It is not necessary, neither is it possible, for each female to have a rival for the territory in which she has settled. Probably it will only occasionally happen that two females meet in competition in any one particular locality, but if, when they do so meet, the stronger gains an advantage, that is all that will be required to maintain the strength of the species.

Our confidence in the truth of a theory must increase in proportion to the number of observations which receive an explanation under that theory, but not under any other. And there are two observations which become intelligible under the theory of breeding territory, but which, hitherto, have been inexplicable. The first of these, and the more important, is the fact of the males arriving at their breeding haunts before the females. It has long been recognised that amongst the migrants the first individuals to reach their destination in the

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spring are almost invariably males. I have met with one instance only in this district of a female arriving before a male. In reference to this, Gätke writes in his "Birds of Heligoland" as follows: "In the spring in the case of all species the most handsome old birds are invariably the first to hasten back to the old homes as the heralds of reawakening life; these are soon followed by the old females, whose numbers increase, while those of the males decline, and the migration is brought to a close by the younger birds." It must not be understood from this that the migration of the males is completed before that of the female commences, but that the migration of the sexes overlaps, males continuing to arrive with females. It is important that this should be clear, because there seems to be an impression that the times of migration of the sexes are distinct, that the males arrive, and that after a pause the females follow. For instance, the late Professor Newton, referring to this peculiarity, says: "It has been ascertained by repeated observation that in the spring movement of most species of the Northern Hemisphere the cock birds are always in the van of the advancing army, and that they appear some days, or perhaps weeks, before the hens." And he then proceeds to give this explanation: "It is not difficult to imagine that, in the course of a journey prolonged through some 50° or 60° of latitude the stronger individuals should outstrip the weaker by a very perceptible distance, and it can hardly be doubted that in most species the males are stouter, as they are bigger, than the females." Had he known that the migration of the sexes overlaps, that a few males arrive, forerunners of the advancing army, but that afterwards males and females arrive intermingled, it is probable that his interpretation would have been modified. And even if it be granted that the males are the stronger, this cannot account for their outstripping the females by a week, ten days, or still less by a fortnight in a journey of perhaps 1,500 miles. To expect them to accomplish such a distance in from four to five days is surely not estimating their

capabilities too highly, and any slight inequality in power of flight or endurance could give the males an advantage of but a few hours only. Darwin believed that the difference in the periods of their arrival could be explained thus: "Those males," he writes, "which annually first migrated into any country, or which in the spring were first ready to breed, or were the most eager, would leave the largest number of offspring, and they would tend to inherit similar instincts and constitutions." But why should those males that first migrated leave a larger number of offspring? Reproduction could not commence until the females arrived, consequently the males that reached sexual maturity later and travelled in company with the females would have equal, if not greater, opportunities for securing a mate. There is some evidence to show that throughout Nature there is a tendency for the males to reach sexual maturity before the females, but this does not explain why they undertake the journey so much in advance; it makes it, in fact, all the more difficult to understand. For we cannot but believe that a male that had reached sexual maturity would be all the more reluctant on account of its own passion to desert the company of the females and travel on to the breeding grounds, there to await their arrival. The disadvantage in their thus hurrying forward is so obvious that we can only conclude that there must be some advantage correspondingly great, for they, above all others, are the individuals that will be called upon to withstand the rigours of an inclement spring, cold winds, and even blizzards, to which countless numbers frequently succumb. This desertion of the females and anxiety to reach the breeding grounds, which is difficult to reconcile with the belief that the first step towards reproduction is the finding of a mate, becomes intelligible if we accept the principle of breeding territory. Those individuals that hurried forward would, on the average, be more likely to attain to reproduction, for they would have the choice of territory, and the fact of being already in possession when other birds arrived would tell in their favour;

moreover, they would have recovered from the fatigue of their long journey, and would thus be in a better position to struggle when challenged by a later arrival ; Nature's process is therefore a simple one, requiring no recognition on the part of the males of territories as such ; their whole behaviour can be accounted for otherwise—and, what is more important still, without our having recourse to complex principles of explanation.

A male, however, does not always have to fight for its territory. It happens, and not infrequently, that its rights to ownership are recognised, and only when these rights are disputed, either by a later arrival, or by another male arriving simultaneously, does a struggle ensue. Thus we have the spectacle, as in the case of the Blackcap, of two or three males following one another for a short time after their arrival, finally separating amicably and taking possession of adjacent territories.

A truer definition of the order of migration would be this : Some males arrive before others, and some females arrive before others, but males arrive before females. The same factor which causes males to arrive before females is possibly the cause of the discrepancy in the time of arrival of the individuals of both sexes. We can of course say of the females, as we can of the males, that the earlier arrivals are probably the more vigorous ; but this does not explain, any more than in the case of the males, why one individual hurries off before another. Moreover, if we accept such an explanation, we are at once faced with a difficulty, and a very considerable one, namely, that the stronger females and the weaker males will travel in company. And if, for the moment, we assume that territory has no control over reproduction, what incentive would there be for the stronger females to seek the stronger males scattered throughout the different districts, and consequently what could possibly prevent their breeding with the weaker males, thereby frustrating the very result for which we all believe Nature is for ever striving, the mainten-

ance of the strength of the species? And if territory *is* an essential to reproduction, and the final appeal for territory is to the strength of the individual male through the law of battle, of what use could it be for females to arrive before males? On the other hand, if the first step towards reproduction is to find an unpaired male in possession of a territory, what would be the position of a female that, from one cause or another, was late in arriving at the breeding grounds? The balance between these extremes, that is to say, between a too early and too late arrival, must have been gradually adjusted to suit the needs of different species.

The second observation is that which has reference to the banishment of the young by the parents. It is well known, in the case of many species, that the parents drive away their offspring as soon as they are able to take care of themselves; and the reasons generally given for this behaviour are, firstly that the supply of food would not be sufficient to maintain both old and young, and secondly, that interbreeding would thus be prevented. While it is no doubt true that both these ends will ultimately be attained, yet neither one nor the other can be the motive force which impels the parent birds to act in so arbitrary a manner, for each would imply an amount of forethought of which no bird is capable. Must we then regard the habit as a chance variation, which, having once arisen at some early stage in the history of bird life, was perpetuated, owing to its having been of some direct benefit to those species possessing it? Or is it not possible that it is linked with some other mode of behaviour? The latter appears to me to be the more probable alternative, and it is by no means unlikely that it has its origin in, or rather is an extension of, the law of territory. As in so many cases, an interpretation is rendered the more difficult by the fact that the habit is not a universal one, but seems to be confined to certain species only. The Moorhen treats its young, when they are able to find food for themselves, with scant affection, pursuing and pecking them unmercifully, and the Stonechat will not allow

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its young to remain in its territory. The instinct is better known, perhaps, in connection with the birds of prey and the Raven; and in some cases it seems to be deferred until the following spring; young Partridges, for example, remain with their parents throughout the winter. Hitherto, I have not been able to trace it amongst the Warblers. Whether it is more prevalent amongst those species that rear two broods, or whether it is limited to those that remain more or less in one particular territory throughout the year, we do not know. A Warbler deserts its territory as soon as the young are reared, but the Moorhen as a rule continues in the same place during the winter months. A migratory species would have nothing to gain by driving away its young, for although it is likely that both old and young return to the same district the following spring, yet it is not probable that the young would lay claim, even if the parents did so, to the identical territory in which they were reared. But the case is different with the Moorhens; they remain in or near their territory throughout the year, and if they allowed the young to remain with them it is unquestionable that, as the sexual instinct arose the following spring, they would have serious rivals in their offspring, by that time fully developed, and in strength equal to themselves. There is much evidence to show that in many cases parental affection is limited to the period in which the young are helpless, and so the natural result of the law of territory would be the banishment of the young; and if in addition the habit was of indirect benefit to a species by preventing interbreeding, or by securing an ample supply of food, then it would be fostered by selection and developed in so far as it was beneficial.

What, then, is the meaning of this law of territory? Why should one male struggle so fiercely with another for a small plot of ground? It is claimed *only* at the breeding season; it is adhered to in many cases *only* so long as there is a nest and eggs or young within its limits; it is of such importance to the individual male that it may even lead to

a fatal struggle; and if a territory is won a mate is won also. No fact has impressed itself upon me more strongly than this latter, for we know that not all the males, nor all the females, arrive at the same moment, and so it happens that one male will commence to breed a week, a fortnight, or perhaps a month before its neighbour; yet notwithstanding this difference in time, which, when we take into consideration how short is the whole period of sexual reproduction, is a very considerable one, I have not found a single case of a male securing a territory and not ultimately securing a mate. It may be urged that the evidence of so small a number of species is insufficient, but let it be remembered that I have purposely studied species very widely separated in the phylogenetic tree, and have found a similar law in operation; and if it were not a general rule that territory and reproduction were synonymous, some instances, some evidence at least, ought to have come under my notice. It seems evident, therefore, that a territory is essential to the individual male if it is to attain to reproduction, and inasmuch as the final appeal for possession is to the law of battle, we can well understand that on the average it will be the stronger birds that will leave offspring to inherit their congenital tendencies; the weaker will either perish, or which amounts to the same thing not attain to reproduction. At the same time we must not always assume that the bird that is defeated is, although weaker, not so fit to reproduce, or not so likely to produce healthy offspring, since it is quite conceivable that up to a certain age the older birds will have an advantage, due solely to laws of growth, but, *on the average*, it will be the stronger individuals that leave offspring. Thus there is constantly at work each recurring spring a process of elimination, whereby the species is not only maintained in a healthy condition, but is gradually being brought to a greater state of perfection. And so in its immediate results, the law of territory is nothing more than a form of natural selection. Before going further, however, it will be necessary to

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state the position with regard to the theory of sexual selection, for, as I shall presently show, a struggle for territory is not compatible with one part of that theory.

The theory of sexual selection really contains two distinct propositions; in the one the male is represented as attaining to reproduction by conquering other males, while in the other by directly exciting the pairing impulse of the female. The first of these is the law of battle, to which is attributed the greater strength of the male, the development of the antlers of the stag, or the mane of the lion, since it is only the better equipped males that will conquer, and thus be enabled to reproduce and leave descendants similarly endowed, and differs altogether from the second proposition, which refers to a peaceable process, whereby it is claimed that vocal and instrumental music, plumes, and colours in birds have been developed owing to the fact that the males, which possess a greater development of those characters excite the females in a higher degree, and are thus more likely to attain to reproduction. This second proposition leaves no scope for the law of battle. Inasmuch, therefore, as they ignore or regard as of secondary importance the desperate and frequent struggles in bird life, while at the same time pleading the immense importance of similar struggles amongst the mammals, the advocates of sexual selection are not consistent, for I cannot believe that such battles have, in the one case, decided the question of reproduction, but in the other in no way influenced it. Moreover, they admit that the conflicts at the period of sexual activity are not confined to mammals, but that they occur amongst the lower vertebrates, amongst beetles and crustaceans, amongst some insects, and even amongst some birds. And I therefore submit that, on their own showing, it is highly improbable that this scheme by which the male has attained to reproduction, the standard of efficiency of the species has been maintained, and the position of the species improved in its relation to the struggle for existence—a scheme elsewhere so uniform

—should have been interrupted in the case of many birds, butterflies, and certain other insects, and replaced by one that does not necessarily imply any greater capacity for resistance on the part of the species in the inevitable struggle. When we actually see, or even reflect upon, such animals as stags or lions engaged in mortal combat, we cannot help being impressed with the grandeur of the scene, and, consequently, we give to those encounters the attention they deserve. But the conflicts between small and inconspicuous birds are apt to escape our attention, and not have an equal share of importance assigned to them. Yet of the two I know not whether the conflicts in bird life are not more strenuous and fierce, do not more often terminate fatally, and have not in the past exercised a greater influence in their own particular sphere. After witnessing these frequent struggles in bird life I confess to feelings of some astonishment that so little regard has been paid to them as a factor in the evolution of bird life. It is also stated—and it is an assumption which is necessary for the theory—that a female shows an active inclination or disinclination for a particular male. Surely this is not a very satisfactory explanation, for it shows signs of that tendency, so fatal to a proper understanding of animal subjective states, to resolve all their activities in terms of human analogy. But we have already seen that amongst a number of migratory species not only is there no evidence in favour of this same predilection, but that there is considerable evidence against it, for if a male gains a territory it gains a mate ; and there is no reason to suppose that they differ in this respect from other species, except that by virtue of the fact of the males arriving before the females we are enabled to arrive at a more accurate interpretation. And supposing that a female were really attracted by one male more than by another, then, in the natural course of events, cases of possession of territory not leading to reproduction ought to be of not uncommon occurrence, for so long as it *does mean* reproduction, any special individual attractiveness to effect

the same purpose is unnecessary, or, to state it in another form, the primary object of the law of territory to the individual male is to enable it to secure a mate; it is a form of natural selection in so far as the stronger males only, on the average, will produce offspring, but this form of natural selection can in no way account directly for the development of the colouring of the feathers, vocal powers, or gorgeous plumes. The primary object of sexual selection to the individual male is also to enable it, by reason of any particular attractiveness, to secure a mate, and it thus attempts to explain the development of those secondary sexual characters. But there never could have arisen in Nature, *pari passu*, two wholly dissimilar struggles, both having the same purpose in view—namely, the attainment of reproduction by the individual. This, as it seems to me, is the position with regard to the second proposition of the theory of sexual selection, and I fail to see how it can by any means be possible for the one process to work with advantage side by side with the other. And if it be asked whether it might not be possible for there to be a further selection by the females of those males that were victorious in battle, I should reply as follows: Firstly, that such a selection would presuppose a large preponderance of males, which supposition would by no means be justified, especially when we bear in mind the fact that even the assumption that males are in the majority rests on no very secure foundation; secondly, that, inasmuch as *ex hypothesi* the more demonstrative males must always be the stronger, a law of battle to attain the same end would be superfluous; this requires further explanation. That the female prefers one male before another on account of some special adornment is not now regarded as probable by those who still hold to the theory of sexual selection as affording the most reasonable interpretation of the facts, but that she is unconsciously excited by the one that is the more demonstrative, and that the demonstration is in proportion to the strength and consequently to the development

of the secondary sexual characters. If this were really true, the weaker males would thus be eliminated and an appeal to the law of battle unnecessary. Thirdly, that it is almost inconceivable that such terribly severe struggles should have been developed if they were not of some direct benefit to the victorious individuals; and, lastly, that in the event of such a further selection taking place, cases of males possessing a territory and yet not attaining to reproduction ought, as already pointed out, to be of not uncommon occurrence. And, having regard to the very meagre evidence upon which is founded that part of the sexual selection theory which would refer the victory to those males that were enabled to excite the females in the highest degree, and considering, too, the very strong evidence in favour of the question of reproduction being decided by a law of battle, it is difficult to resist the conclusion that the latter is the means by which the weaker individuals have been debarred from transmitting their defects to the race.

The fighting of the females, if it can be shown to be characteristic of a number of species, will have an important bearing on this whole question. In discussing the theory of sexual selection in the life of the Grasshopper Warbler, I stated as one of my principal objections to that theory that the ultimate production of the most healthy and most beautiful offspring by the selection of certain males is, without a corresponding selection amongst the females, impossible, and of the existence of such a selection in any form there is no evidence; and upon this point I see no reason to alter my views. In fact, further consideration seems to me to add to rather than detract from the force of this objection. For it must be borne in mind that what we are in reality aiming at is the maintenance of the strength of the species, and in thus stating my objection I wished to make it clear that in order to attain this end an elimination of the weaker females is as necessary as an elimination of the weaker males. Strength and beauty cannot be separated, and even if it were ultimately proved that there

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were no commingling of the colours as a result of amphimixis and that, consequently, a dull-coloured female could not directly influence the colour of the male offspring, yet this would not affect the issue, for vitality must react upon the colour and influence the growth of the secondary sexual characters. Evidence of this can be seen in our domestic animals, and to some extent even in ourselves. A dog in a low condition of health loses the brilliancy of the colouring in its coat, and, as is well known, the colouring of the human hair is affected by ill-health. But if a law of battle obtains amongst the females, we need no further explanation as to how the standard of efficiency has been maintained through numberless generations.

We have discussed the meaning of a territory to the individual, and have come to the conclusion that it is the attainment of reproduction; but inasmuch as this same result could be gained equally as well without all the complications introduced by a territory, it is evident that by this means some larger purpose is being fulfilled. That a breeding territory is of immense importance we can infer from the fact that we find the individuals of such widely separated species as the Falcons, Warblers, and the Moorhen struggling for possession. For my part I believe that the question of food supply has been one of the determining factors, although there are two observable facts which are somewhat opposed to this view. Firstly, that the members of any one of those species referred to, while objecting so strongly to a member of their own species breeding in their territory, frequently ignore the presence of one of another species, no matter how closely allied it may be, and no matter whether it would require a similar food; and, secondly, that there are a number of species that breed in communities. But upon further consideration these difficulties will be found to disappear to a great extent. It is true that in Nature we can find more than one species, requiring similar food, inhabiting the same small area of ground. But supposing the law of territory were temporarily suspended,

then there would be nothing to prevent any number of the same species congregating within a very restricted area. Consequently the food supply, which might have been ample for the progeny of one pair of each of those species, would become exhausted in the immediate vicinity of the nest. The parent birds, therefore, instead of seeking and finding food close at hand, would be compelled to travel further and further afield, and thus the quick supply of food, so essential to the welfare of the offspring, would not be forthcoming, and correspondingly the interval for brooding, which is of such importance during the early stages of growth, would be diminished, with results that could only be detrimental, and in cold wet seasons disastrous to the offspring. Apart from these general considerations, my belief that the effect of this law of territory has resulted in securing an efficient food supply for the offspring in their early stages of growth is based, in some measure, on the behaviour of certain birds, both at the commencement of the period of sexual reproduction and after the young are able to take care of themselves. If a pool, surrounded by agricultural land and occupied by a number of Moorhens, is kept under observation early in the season, it will be noticed that each morning at daybreak the different individuals will wander over the land in search of food. Now select some one particular pair, owning a territory, and notice their behaviour. Any intrusion upon their domain is resented; it is only necessary for an unpaired individual, wandering amongst the rushes, to overstep the boundary, to call forth a peculiar cry from the owner, followed by a determined attack. Presently one or two individuals or pairs fly or run out on to the fields to feed, causing a stir amongst the whole community; one bird follows another, the pair we are watching swim towards the shore, join their neighbours, and in company with them peaceably search for food. The fields are clearly regarded as neutral ground, the territory itself being probably not capable, so early in the season, of supplying the owners with food. But when the young are hatched, the conditions

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are different, aquatic insects being then plentiful, and young succulent aquatic plants abundant. Or take the case of the migrants after the young are reared and able to take care of themselves: the parent birds do not still remain in their territory, but frequently separate and wander from place to place with no fixed abode. It cannot therefore be the desire to secure an efficient supply of food for themselves that causes the Moorhens to defend their territory so stoutly, since they seek for and find much of it upon neutral ground. Nor can it be anxiety to prevent the possibility of lack of food for themselves that impels the Warblers to struggle together, for why then should they desert the territory they have won and so consistently defended as soon as the young reach a certain age? As I shall presently mention, the Reed Warblers do seem to regard the tops of the alders surrounding the reed bed as neutral ground, resorting thereto to seek food for their offspring. But their territories are small owing to the comparative scarcity of suitable breeding grounds, and some relaxation of the general law may be advantageous in their case.

Glancing at an early period in the history of bird life, we are now in a position to understand partly what may have taken place. Those members that were not pugnacious, and thus allowed others to breed in proximity to them, would certainly attain to reproduction, but their offspring, if they did survive, would be weak owing to lack of food and exposure to changes of temperature, and in their turn would produce a weakly race unfitted to struggle, when called upon to do so, with stronger individuals, and so the tendency to sociability, having in such cases no opportunity for expansion, would gradually disappear. But the necessity for a supply of food in the immediate vicinity of the nest would not always have been imperative, and in some cases might not have been of sufficient importance to outweigh advantages gained from a number of individuals congregating together, so that we should then find members of one species breeding in a community.

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But with respect to this law of territory we must still regard a community as one unit, for community fights with community as one individual fights with another. The Rooks from one rookery will attack those from another, the members of one colony of Gannets (*Sula bassana*) will struggle with those of another. And it is possible that the attainment of reproduction may be an even more difficult task for those species that are sociable, since battles occur between individuals with respect to their own particular domain even within the precincts of the territory of a community. At no time are the Rooks so quarrelsome as when they commence to build their nests, and though the quarrel may be only caused by one stealing nesting material from another, yet they certainly appear to respect one another's rights. But even the stealing of twigs and wool would be similar in its results to a battle, if thereby any particular individual were prevented from breeding. Circumstances compel other species to breed together. For many sea-birds breeding stations are few and far between ; nevertheless, even the members of these cliff-breeding species seem to have their own particular territory ; and it must be remembered that not every Gull nor every Guillemot on a ledge of rock is a breeding bird. The working of the law of territory is a beautiful illustration of adaptation, since a territory is developed in some instances to ensure an ample supply of food for the helpless young, while in others it is gradually limited in extent to ensure reproduction, but in every case perfected so as to hamper in no way, but rather improve the position of the species in relation to the struggle for existence. Thus scarcity of breeding stations, scarcity or abundance of certain types of food, and the relation between the supply of food and the localities suitable for breeding purposes must have been taken into consideration as species arose and adjustments were made accordingly. If the individuals of any one species were to develop a territory larger than was necessary, and by so doing prevent a portion of their own community from breeding, that species would gradually

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be eliminated just as surely as one whose members did not secure sufficient ground to ensure an ample supply of food for their young. But it is clearly impossible to trace the history of the development of the breeding territory unless we have before us a true phylogeny, and the conditions under which the earlier types existed. Many of the sea-birds, which breed upon ledges of rock, are compelled to travel some distance before they can find a situation suitable for rearing their offspring, whereas the question of food presents no great difficulty; consequently the limits of their territory have been reduced to the minimum size necessary for reproduction. In a case in which the territory has been developed in order to ensure an ample food supply during the period of reproduction, it is possible that the area of that territory, and consequently the numerical strength of the species, will be found to be proportionate to the distance its members are accustomed to travel in search of food. This, in some instances at least, appears to be the case. Those species that have long distances to travel are represented by comparatively few, and conversely those that find food close at hand by numerous members. The birds of prey wander over a great distance, consequently their territories are large, and the same may be said of the Raven. It is not every tree that can supply the necessary food for the Woodpecker—in fact, such trees are relatively scarce—therefore it has first to search for and find the suitable trees, and then it will visit them daily, generally in routine, covering a considerable area while so doing. At the same time it by no means exhausts all the possible food supply; the area covered would possibly be sufficient to maintain one other pair at least, but by reason of the fact that the food is difficult to find the distance traversed may be beyond what is really necessary. In such a case the conditions of existence might be so strenuous that it would become of the utmost importance to any particular individual to prevent, not only members of its own species but also those of closely allied species, from breeding in the

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same territory. This may have been the cause of a struggle I once witnessed, towards the end of May, between two Lesser Spotted Woodpeckers (*Dendrocopos minor*) and one Great Spotted Woodpecker (*Dendrocopos major*); the latter bird defending a decayed tree, in which possibly its nest was situated, against the onslaughts of the former birds. I have recently gained some further evidence upon this point, for I had an opportunity of watching a conflict between a Great Spotted Woodpecker and a pair of Green Woodpeckers for the possession of a hole in an oak tree. The struggle was carried on intermittently for some days, and as far as actual strength was concerned the Great Spotted Woodpecker was no match for its rivals, but remarkably persistent, and although pecked mercilessly whenever, in the absence of the Green Woodpeckers, it took possession of the hole, yet it refused to leave the locality. Struggles between closely allied species may in reality be of more common occurrence, and may exercise a greater influence, than is generally supposed; amongst the Warblers at least there is no doubt that such is the case, for Willow Warblers and Chiff-chaffs on the one hand, and Blackcaps and Garden Warblers on the other, are constant rivals.

The limits of a territory must be influenced by the conditions of existence of the species. Swamps overgrown with the common reed (*Arundo phragmites*) not being found everywhere, the territory of the Reed Warbler is consequently small, and has, no doubt, been reduced gradually to the minimum size necessary for the welfare of the species. If the dimensions had been similar to those of the territory of the Chiff-chaff, the species would have rapidly disappeared. Hence there is a point beyond which a species in any one particular district cannot increase, no matter how favourable the conditions of existence may otherwise be. Nevertheless it is probable that this point will seldom be reached, for I can well imagine that the very fact of territory being of such importance as to necessitate one male fighting with another

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for possession would lead to available breeding ground remaining untenanted. For a male when seeking a territory will settle by chance in a certain place, and finding it already occupied, will struggle with the owner, and perhaps be defeated, or quietly pass on. In either case it may lay claim to adjacent unoccupied land, but it is not unlikely, especially after a fierce encounter, that it will be only too anxious to abandon that immediate district, thus leaving available ground in its rear unoccupied. Every male will not be compelled to struggle each season for its territory; it is clearly impossible that it can be so. On the other hand, if every male has always equal chances of securing a territory, and thus attaining to reproduction, no elimination can take place and no beneficial results can accrue to the species. But this will not be the case; competition will vary in different species, will vary in different seasons, and even in the same species will vary in different districts, according to changes of environment and the rate of increase. The weaker males will often reproduce, but, taken over a number of years, the stronger will reproduce more often than the weaker, and this is all that is required by the theory.

When we consider all of this, and at the same time bear in mind that the reproductive instinct is possibly not so strong in one male as in another, so that in the former case it may soon become weary of seeking territory and be content to remain unobserved in a district already tenanted, we can understand that there must needs be a number of unpaired birds. The pool in front of my house is generally inhabited by one pair of Moorhens. One autumn both birds disappeared, the one some time after the other. The pool then remained unoccupied until the 16th of the following June, upon which date a single individual took possession. On July 13th a mate appeared, and they immediately commenced to build a nest, ultimately succeeding in rearing a small brood. If territory were not a necessity, why should these two solitary individuals of the opposite sex have waited till so late in the

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season before commencing to breed? And is it not suggestive that breeding operations commenced so soon after the pool was discovered by the first individual? To Darwin it was somewhat of a mystery how it came about that within the same district during the height of the breeding season there should be so many males and females always ready to repair the loss of a mated bird, and in the "Descent of Man" he gives the results of experiments showing to what an amazing extent new mates will be forthcoming—results which from my own experience I believe to be in no degree exaggerated—and he considered that an explanation might be found in the fact that certain males and females do not succeed at the proper season in exciting one another's love, and consequently do not pair. Which are we then to believe—that males seek the females, or that the females seek the males? Or must we assume that a mutual search takes place, the sexes wandering about on the chance of ultimately discovering a suitable partner? No one who has studied the habits of the migratory species can seriously entertain this latter possibility, for whether the principle of breeding territory be accepted or not, this fact is patent, that the males settle and remain in a certain restricted area even before they are paired. Therefore if one sex does really seek the other, it can only be the females that seek the males. But since we see, on the one hand, a proportion of the males settling in their respective territories and there remaining, and since on the other we know that a proportion are wanderers with no fixed abode, and find that the males that remain in one place invariably secure a mate, while those that are wanderers appear to be always ready to pair when an opportunity arises, surely a more simple and more probable explanation of the fact that certain birds remain unpaired is afforded by the law of territory, the unpaired males being those which have been unsuccessful in securing a territory, the unpaired females those which have been unsuccessful in finding unpaired males in possession of a home. A curious feature with regard to the unpaired birds is

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that, in the case of many species, they are so seldom in evidence. But this we can understand if we remember that such birds would be restless wanderers, not resident in any one particular locality, but continually being urged to move from place to place by their sexual instinct; and, if at any time they should happen to be in or near a territory already occupied, they would be, no doubt, desirous of concealing their presence. This fact of the unpaired birds being so seldom in evidence, while at the same time so numerous, is one of some importance. It emphasises the close connection that must exist between territory and reproduction, for if there is no law of territory how can their behaviour be explained? Why should not the unpaired males instead of wandering about, apparently wishing to remain unobserved, be content to stay in one particular locality and make their presence known by song, as the majority of the males do who secure mates?

Many species have extended their breeding range in recent years and are even now extending it. It may be said that this extension is not real, but only apparent, owing to the greater interest taken in Nature by a consequently greater number of competent observers, so that whereas formerly a species, although present, remained unobserved, at the present time it is immediately detected. There is no doubt some truth in this, but at the same time there is strong evidence to show that in many cases the breeding range has unquestionably been extended. If the extension were limited to those species only whose numerical strength was exceptionally great, it would not, perhaps, be quite so surprising. But this is not the case; even those that are not numerous are slowly but steadily increasing their range. There is no direct necessity, so far as reproduction is concerned, for a bird to desert the particular neighbourhood in which it was reared; in fact, there would seem to be an advantage in its not doing so, since there would be a greater likelihood of securing a mate in a district already inhabited by the species; neither is there any

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reason, so far as we are able to judge, why, in many instances, more members should not breed in proximity to one another than actually do so at the present time. Have we not an explanation in the constant struggle for territory—that struggle which is such an essential to reproduction, a motive force, as it were, dispersing the species in every direction? But let this, which I have already pointed out, be remembered, that the territories need in no sense be regarded as a chain with numberless links, and that it is not essential for every available plot of ground to be occupied before the species can extend, but that by reason of the struggle being so relentless it must happen, and not infrequently, that an individual will be unnecessarily urged to seek ground beyond the immediate neighbourhood.

Now there is no reason to believe that this struggle for territory has only recently arisen. Possibly it has been even more severe in the past. But if proof of its early origin be required it can be found in this fact, that it is severally common to and inseparable from the habits of widely separate species. Therefore let us glance at the past history of an imaginary species, and, bearing in mind the severity of the struggle on the one hand, and the long periods of time on the other, attempt to trace the course of events in so far as they might have been affected by this law. We must suppose that the species is of comparatively small numerical strength, and of limited range, and, further, that a point has been reached when the individuals that do not allow others to breed in proximity to them have gained an advantage. Each recurring spring the conflict for territory would take place, causing an extension in the breeding range. In some directions the conditions of existence might be such as would make it impossible for the species to survive, in others large areas might be unoccupied, owing possibly to their being passed over unheeded, or to the individuals settled therein having been from one cause or another exterminated and not replaced, and yet in others the succession of breeding territories might be con-

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tinous. Thus the range would be gradually extended further and further from its base until it began to advance into regions subject to alternations in climate, and in which, consequently, the duration of food supply was more or less limited to a few months in the year. Whenever this point was reached, it would be necessary for the individuals to return for part of the year within the zone of perpetual food supply. Now we know that, in the case of the migratory species, there is a strong propensity in the individual to revisit in the following breeding season that particular neighbourhood in which it was reared. But even if we did not know this we should infer that it was so from our knowledge of the conditions under which the range of the species is being extended, *i.e.*, from the law of territory. For if those males that were forced to desert a certain district through insufficient food supply during part of the year did not again go forward the following spring to their former breeding haunts, overcrowding would occur at some point ; and inasmuch as reproduction would be impossible to a large and increasing number, owing to lack of territory, the distribution would remain stationary, and a check would be administered to the welfare of the species. Therefore any variation in the direction of a tendency to return would be fostered and developed by selection. And so it would be with the females ; those that did not return to their birthplace, or their old breeding haunts, would be less likely to reproduce, since they would have greater difficulty in finding an unpaired male in possession of a territory. We can then understand that the range of our imaginary species would be extended with a corresponding increase in the distance traversed by some of its individuals between the zone of perpetual food supply and the breeding haunts, until the limit imposed by unfavourable conditions of existence were reached. And when we consider the conditions under which it must have existed, the constant struggle and constant search for new breeding grounds, changes in the earth's surface, and changes of climate, resulting in the gradual disappearance of

the individuals in some parts of the globe, we can see that it is more than probable that many districts, formerly inhabited, would not be inhabited to-day.

In applying this law of battle to the life-history of these smaller species, I am only extending a principle which is already recognised as a factor in the evolution of animal life. But in positing territory as the primary cause of the struggles I am departing from the prevailing opinion. And inasmuch, therefore, as this is the point which is the more likely to be disputed, it will be as well if we review once more, but briefly, the evidence upon which it is based, and in so doing we shall see how impossible it is to reconcile the facts with the only other possible explanation, namely, that the females are the direct cause of the struggles. In the first place, then, we have this fact established, that in the majority of instances each individual male of the migratory species when it finally reaches its destination, and each individual male of the resident species when the sexual instinct commences to develop, and in some cases throughout the year, remains in a certain restricted area encompassed by well-defined boundaries which it seems unwilling to cross. Next we have the spectacle of these same males engaging in fierce conflicts amongst themselves, and in the case of the migratory species even before any females have arrived; and this one fact, if placed beyond dispute, would alone be sufficient to show that the females are not the direct incentive to the struggles. But as the plea of insufficient observation may here be raised—and no one can deny that a female skulking in the undergrowth might easily escape detection—we will pass on to the behaviour of the males after the females have unquestionably arrived, and we find them still continuing to struggle after pairing has taken place, after the nest is built, and even after incubation has commenced, though with less and less determination as the season advances; and, moreover, we can observe that these quarrels follow after, and not infrequently seem to be con-

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sequent upon, one male crossing its boundary and entering the area of its neighbour. And, lastly, in the case of two males occupying adjoining territories, one paired and the other unpaired, we find that the unpaired male frequently attacks not only the neighbouring male but also the female when either of them intrudes upon its territory. Any one who will take the pains to keep under observation two pairs of Chiff-chaffs, or of Blackcaps, living in proximity to one another, or, better still, some large sheet of water inhabited by a number of different pairs of Moorhens, can observe for himself these struggles which are of almost daily occurrence. And how great an influence they must have exercised upon the history of any one given species we can well imagine, when, on the one hand, we remember how incessant they must in reality be in order that we may so readily observe them, and, on the other, bear in mind the enormous period of time through which species have been slowly evolving.

The strength or weakness of the theory lies in the evidence upon which it is based, that is to say, upon the observation of one person, and herein, at least, lies a weakness. But although it is probable that in the details there may be some exaggeration—and it is doubtful whether the human powers of observation are capable of always giving an accurate statement of the facts—yet the essential facts I believe to be true; and I appeal to Nature herself for corroboration. Let these principal points be borne in mind: that whatever species I have hitherto studied I have found the question of territory in some degree present; that the problems with regard to unpaired birds, rate of increase, extension of breeding range, and, in the case of the migrants, the hurrying forward of the males in spring, on this principle become capable of solution, and once more, and finally, that although the evidence is drawn from the lives of comparatively few species, yet some of those species are not closely allied, but belong to widely separate genera.

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To return to the Reed Warbler. The females often commence to arrive shortly after the first males, but how soon after depends upon whether the arrival of those males was an early one or the reverse. They are seldom in evidence before the middle of May, so that if a male arrived at the very commencement of that month, fully a fortnight might elapse before pairing commenced. As already mentioned, the period of migration of both sexes is spread over a considerable time. The female that arrived on June 21st must still be regarded as a migrant, although it is quite possible that this particular bird, as also, perhaps, many of the males that are very late in arriving, was only a wanderer in this country, not a true migrant in the sense of having only recently completed its migratory journey. However, it is quite impossible to decide this; the wandering males may only be the individuals that have been unsuccessful in securing a territory, the wandering females those that have been unsuccessful in finding an unmated male in possession of a territory. The fact of these observations having been made in the centre of England makes such a contingency more possible than if they had been made on the south or south-east coast. But whether it be the case or not, it is evident that solitary males, forerunners of the migratory movement, are the first to reach this country, and in this respect the species resembles other migratory species. The interval between the arrival of the first male and the first female may vary in different species; and, if this is so, we should expect it to be of shorter duration in the case of those species that are accustomed to reach this country in May than in those that face the cold winds of March.

The period of sexual activity is disappointing so far as the attitudes assumed are concerned. There is no abnormal waving of the wings and spreading of the tail, which is characteristic of so many species. We may say that the nervous organisation of the bird is not so highly developed as that of some others, and thus attempt to account for the difference, but this does not take us very far towards a

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solution. If we thoroughly understood the development of the sexual organs and the influences exerted thereby, the explanation of these activities might be less of a mystery than it is at the present time.

The unemotional behaviour of the male Reed Warbler at this period is, then, very striking. He follows the female closely from place to place as she wanders about his territory, giving expression to his feelings by occasionally bursting into song, or by flying at and playing with her, fluttering amongst or over the tops of the reeds, sometimes even pursuing her rapidly. In the moments of extreme excitement he sings rapidly, raising the feathers on his head and back, and loosely fluffing out those on his breast and flanks while doing so. He also spreads his tail, and slightly raises or rather jerks his wings. Once only have I seen a male, previous to the actual construction of the nest, carry, while following his mate, some material in his bill, and in this instance he appeared to be carrying some seeds of the bulrush. How far the duration of the period of sexual activity varies in the case of different individual pairs I am unable to say. But it is not very probable that the species differs in this respect from others. Judging from those instances which I have had under my notice from the commencement of the breeding season, this period would seem to be of short duration, for the nest in one case was actually commenced the very morning upon which the female arrived. Although the male sings frequently when following the female, yet his song is not so persistent as prior to her arrival. The male that had his headquarters in the *salix* bush sang morning after morning for a whole month until a female arrived, when he almost deserted the bush and became comparatively silent.

The nest, when built amongst the common reed, is suspended from stems varying in number from three to seven, but it is sometimes placed in a young alder tree (*Alnus glutinosa*) not more than 5 ft. in height, or even amongst the branches of willows. But this latter situation seems to be resorted to when

the reeds, or rather a territory including reeds, are not available. When the opportunities of building in the willows fringing the reeds, or in the reeds themselves, are equal, the latter situation seems to be chosen in preference. I have examined a number of nests for the purpose of discovering whether, in their construction, new reeds were made use of more frequently than old, and whether both new and old were utilised at the same time ; for it occurred to me that, if the latter were the case, the growth of the new reeds would cause the nest to become tilted on one side, and bring about a calamity by precipitating the young into the water. All three methods, I find, are followed, although of the nests examined only one was built upon both old and new reeds ; this, however, must not be regarded as a correct proportion, the number examined being much too small to enable such a proportion to be correctly estimated. As a rule the nest is attached somewhat loosely to the stems, and it might thus be able to slip and automatically adjust itself to the growth ; but there are budding leaves on the new stems, and an uneven surface and joints on the old, which might at any moment prevent its slipping and result in a gradual tilting of the nest to one side. Therefore I am inclined to think that the danger is a real one, but one that is kept in check by selection, and it would in no way surprise me to find that the number of individuals that constructed their nests after this fashion was but a small proportion of the whole. Whether old reeds are used more frequently than new is difficult to determine, since in many places the natural conditions have been altered, the reeds being cut in the winter months and the birds being consequently forced to wait until the new ones have made sufficient growth before commencing to breed. Neither is it possible to say, or even to guess, what the original nest-building instinct of the species was, whether, that is to say, the species as a whole was limited to the use of new or of old reeds, or whether some individuals used the one and some the other. The latter alternative is not impossible, and there may be two races, so

to speak, one accustomed to construct their nests on old and the other on new reeds. And, if this be so, it will to some extent explain the peculiarly erratic arrival of different individuals even in the same reed bed, the earlier comers being those which had adapted themselves entirely to the use of dead reeds. The actual number of stems to which the nest is woven varies very considerably; one bird will make use of three reeds, while another of no less than seven. But the number chosen must have been in the past, and must be still, so regulated as to ensure the safety of the young; and in a case of this description we need have little hesitation in attributing the result to selection. A nest woven to two reeds, if it were possible to construct it thus, would not be durable, and even when woven to three does not always appear to be sufficiently secure, yet this number is sometimes resorted to; and if three reeds be really sufficient, why, in so many cases, should four, five, six, or even seven be used? It may be suggested that where a small number of stems is used it is the first attempt of a young bird, and that as it finds the number insufficient to hold the nest securely, it profits by experience, and at the next attempt adds another and yet another stem. But to profit by experience, persistence, with varying effort, is necessary. "Repetition of trials with variation of procedure is a sort of perceptual experiment. The results of previous experiment determine and facilitate future action, inasmuch as unsuccessful modes of procedure are gradually eliminated and successful modes alone survive."¹ A bird builds a nest but once a year, and therefore the conditions necessary are not really present in a case of this description, and to expect it to realise the cause of the failure of its first attempt, and to overcome its difficulty in advance, would be to raise the level of its whole behaviour from the perceptual to the ideational plane, which I do not for one moment believe we should be justified in doing. And whereas

¹ Stout's "Manual of Psychology."

the whole behaviour is so simply explained by selection, in that those members that did not construct their nest sufficiently securely would be very liable to lose their offspring, we may conclude that this is the means by which the degree of adaptation has been attained.

The nest is a delicate and beautiful structure composed principally of the seed-heads of the common reed. The foundation is formed of the leaves, or pieces of the outside of the stem, of the dead common reed, intermingled with the thinner stems of various rushes woven together with moss and wool, and the interior of seed-heads and small stems of rushes, the lining being entirely of the former. The external part is much the same as the foundation, wool and moss being interwoven. The manner in which the nest is actually woven to the stems is remarkable, and I much regret never having seen the birds at work "laying the first brick," so to speak, for to myself it is a mystery exactly how the initial step is taken. The most characteristic and at the same time most interesting part about the nest is its great depth. Such a peculiarity cannot but be for some purpose, and the reason often advanced is that the eggs are thereby prevented from rolling out when the reeds are bent. I have watched the nest swaying in a wind, and have even bent the reeds for the purpose of finding out how far it would have to be tilted before this would happen, and the conclusion thus reached was that even if it were half an inch shallower the wind would have to be of very exceptional strength before it could bend the reeds sufficiently to bring about such a result; for it must not be forgotten that the nest is not placed at the top of the reeds, but in the centre, three or four feet from the water. If indeed it be true that there is a danger of the eggs thus rolling out, what must we say as to the young? Herein, at least, lies a possible danger. Watch them when a week or ten days old clinging to the nest, the topmost birds level with or even slightly above the sides of the nest, and then imagine the nest itself no deeper than that of the Whitethroat, and the danger will be at once apparent.

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It is remarkable that many, deep as the nest is now, are not precipitated headlong into the water; but their long legs and their innate power of clinging, no doubt make their position more secure than it often really appears to be. The nest is one of those beautiful adaptations of Nature which justly excite our wonder and admiration, for on the one hand it must be sufficiently deep to eliminate all possible risk of the young being thrown out, while on the other it must not be too deep to retard the process of incubation. If the depth were too great, there would be a danger of the young in their early stages of growth not being sufficiently covered with the feathers of the parent bird to ensure their bodies being maintained at a proper temperature. How important this must be in the case of the eggs can be readily understood, but it is even more important—and this can be inferred from the behaviour of the parents—to maintain the young for the first few days after they are hatched at a certain temperature. Sleep is to some extent dependent upon warmth, and sleep is a vital necessity for the helpless naked young; therefore if the nest were too deep they would not be properly surrounded with the breast and belly feathers of the parent birds. Even as it is, the female when brooding appears to me to be in a most uncomfortable position. In the construction of the nest she does the greater part of the work, carrying billsful of the seed-heads of the reeds, which she rapidly fixes, and as soon as the outer part of the nest is completed and it begins to take its proper form, she lies in it and shapes the interior with her breast by turning this way and that, and at the same time often uses her bill to assist in arranging the material in the interior. Her efforts to build the nest are not without what appears to be the usual hindrance caused by the exuberant spirits of her mate, for, while she is at work, he often flies at and pursues her, with the result that there is much fluttering amongst or above the tops of the reeds, with an audible clicking of bills as they meet. Five or six days may elapse between the time when the nest is commenced and the laying of the first egg,

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and as to the period during which the eggs are laid the species does not seem to differ, on the whole, from others closely allied, one being laid as a rule every twenty-four hours. The behaviour of the male, directly the first egg is laid, is interesting, as he at once takes his share in sitting upon and maintaining it at the proper temperature. Judging from their actions incubation proper does not commence until the fourth or fifth egg—according to the number of the clutch—is laid; for directly the full number is completed their anxiety not to leave them too long exposed is very apparent. I have taken particular notice of the behaviour exhibited by the sexes during the period of incubation, and it does not seem to me to show any very striking difference. Nineteen minutes is the longest period I have recorded that the female has remained upon the eggs, and seventeen minutes in the case of the male. The one leaves the nest immediately upon the appearance of the other, and the male will sometimes sing on the way to the nest, and even while on the nest itself. The female utters a low quiet note as she approaches and is desirous of replacing her mate, and whilst sitting upon the nest pecks at and appears to be arranging the material in the interior. There is a difference—but whether such difference is constant, or happens only to have been the case in those instances I have had under my notice, it is impossible to say without further investigation—in the direction in which the sexes face while incubating; each one seems to have its own particular direction, which it adheres to with more or less regularity.

Incubation lasts fourteen days, calculating from the day upon which the last egg of the clutch is laid; and as soon as the young are hatched the parents become decidedly more anxious, betraying uneasiness in their movements. Of the two the male is the more nervous, approaching the nest with great timidity and only with difficulty overcoming his alarm at one's presence. But, as already mentioned, the excitement displayed by the species as a whole, both at this and other

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emotional periods, is as nothing when compared with that of many others at corresponding periods. I cut away the reeds, and even make a clear opening of some few feet in length so as to be able to have the nest in full view, and the female takes but little notice, hesitating only so long as there is any appreciable movement, but if I remain motionless for a few minutes she quietly approaches the nest and attends to the young. Testing her patience still further, I take up a young one, hold it in my hand, and remain with it near the nest, but still she does not respond actively after the manner of the Blackcap or Whitethroat, travelling only from reed to reed whilst uttering her quiet purring note. On referring to my notes taken while watching the nests of various pairs during the last few years, I have been astonished to find that in no single instance is there any record of the male brooding the young. This fact seems so curious that I am almost persuaded that it is an oversight on my part; yet the notes seem to accurately record the actions of the male at the time. It is the more curious when we remember that he takes his share in keeping the eggs at the proper temperature before incubation commences, and that he also shares the duties of incubation equally with the female. If it is really the case, it is somewhat difficult to explain, for if competent to incubate, surely he must be competent to brood, unless there is a difference in the bodily temperature of the sexes; possibly the parental instinct is stronger in the female than in the male.

Brooding occupies the greater part of the time of the female, and is clearly the more important consideration in the early stages of the growth of the offspring, since warmth and sleep, the latter dependent upon the former, are then the necessities of life, food supply being of less importance. But correspondingly with their growth these conditions become gradually reversed until food supply is the greater necessity and warmth of minor importance, a stage which is reached when their bodies are more or less covered with feathers. During these few days the male is by no means idle; he is

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indeed the most persistent of workers, never relaxing his efforts to procure food, which he delivers to his mate or young.

When they finally leave the nest the young are approximately eleven days old. During the first few days of their existence they sleep and receive food, but show little signs of activity ; about the sixth day their feathers are of a considerable length and show the brown colour upon the back. When about eight days old they stretch themselves, flap their wings, and peck at the insects on their bodies, and a day later they are capable of making considerable noise when the parents bring food, and they also begin to make use of the quiet call note. On the tenth day they can be seen preening their feathers, pecking at the insects both upon their own bodies and upon the heads of one another. The stronger individuals now begin to make excursions from the nest, climbing about the surrounding reeds, only to return shortly, and by the eleventh day they are all, as a rule, sufficiently grown to be able to leave.

For the first few days after the young are hatched, brooding is of great importance, and it is consequently left in a great measure to the male to collect the necessary food ; this he seeks for the most part in the reeds immediately surrounding the nest, that is to say, in his own particular territory, hunting amongst the tops or at the base, which, in the drier parts, is a fruitful source of supply. Or if in the vicinity of such trees as alders he resorts thereto in company with members of his own and other species, for the tops of such trees seem to be regarded as neutral ground. When he has thus collected a sufficient quantity of insects he returns to the nest, and upon his arrival the female raises her body while he places the food in an open gape ; or sometimes he delivers the whole or part of it to her, and she may then divide it, swallowing part herself and giving part to the young ; or, again, she may pass the whole of it on to her offspring. So that for the first few days he is often compelled to find food both for his mate and young. She, however, does not brood continuously, but leaves

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the nest for short periods, generally returning with her bill full of insects. About the fourth day the brooding becomes considerably less, and in proportion the supply of food increases, until both sexes are often at work together collecting and bringing supplies. The faeces, enclosed in a membranous sac, are ejected by the young after the food is delivered to them, and are then carried away or eaten by one or other of the parents. If defæcation does not immediately take place the parent touches the youngster's anus with its beak, which usually has the desired effect.

As it is possible to obtain so clear a view of the nest and of the behaviour of the parents, I have been much interested in noticing the method adopted by them when actually delivering food to their offspring. Where there are four or five young in a nest we should expect to find the food delivered more or less in rotation. But this does not seem to be the case. In fact it may happen that both parents arrive at the nest simultaneously with food in their bills, and deliver it into the gape of the same young one, and also that the same bird is fed over and over again until—and this will scarcely be credited—it lies with bill open, apparently too exhausted to swallow so large an amount of food. At other times the insects are divided more evenly, three of the young perhaps receiving food from one parent; and part of it may be even withdrawn from one gape and placed in another.

The young do not all develop with equal rapidity. The growth can easily be watched day by day, and it will be found that the feathers are more developed on one bird than on another, and ultimately that one is ready to leave the nest before the others, and moreover does actually do so, a difference perhaps of one day, or in some cases even of two days, intervening. By the expression "leaving the nest" I do not necessarily mean deserting it, but that the bird is sufficiently developed to make short excursions amongst the reeds, returning again to the nursery; nevertheless, cases have come

under my notice where there appeared to be little doubt that the young did not all desert the nest at the same moment. The explanation must be that the stronger individuals, receiving an unequal proportion of the food, develop more rapidly, and thus are capable of leaving the nest earlier. But what do we mean by the stronger individuals? Is it an instance of the natural selection of those that are more fit? It is a common saying amongst those who are accustomed to take the young of such birds as the Magpie (*Pica rustica*), while still in the nest, in order to make pets of them, that the females are at the bottom of the nest, and the males on top. How far this is correct I have had no means of judging, but it may be a possible explanation. The males would be naturally the stronger, and would therefore require and receive a greater supply of food, and, being the stronger, would struggle until they forced themselves above the females in their efforts to reach the food as it was from time to time brought by the parents. The explanation of the behaviour of the parents and young may therefore be this: that the stronger individuals—possibly the males—require more food and thus are more persistent in stretching up their necks and opening their gapes. And I believe that no one could watch a nest of young from day to day without coming to the conclusion that the most persistent individuals were the ones that on the average secured a larger quantity of food, and that this persistency was the direct factor which influenced the behaviour of the parents; the indirect determining factor being the relative rapidity of digestion in the different individuals and the consequent sensation of hunger. To take an extreme case: a bird that has received a large supply of food will lie quietly in the nest with a tendency to sleep, and when the parent again arrives with food and the remainder of the young stretch out their necks and utter their call-note, will pay no heed, but will remain in an apparently sleepy condition. As the process of supplying food continues, it will gradually rouse itself, at first stretching out its neck with little determination, but finally becoming frantic in its

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efforts to obtain the food. We may then almost say that the whole process is a mechanical one; the parents know not, neither could they possibly recognise that one individual is stronger and thus would demand more food than another, still less could they possibly comprehend the difference being a sexual one, if indeed it were so. Their behaviour is solely determined by the organic response of the young. It is not necessary for them to consider—nor do I believe that they would be capable of doing so—a matter so abstruse as supplying food in rotation; it is not even necessary for them to remember to which individual they delivered the last supply of food, although it is not improbable that they sometimes do so. After watching the routine of different pairs under similar conditions, I can see no reason to believe that they in any way profit by experience. How far their whole behaviour may be congenital, or how far traditional, it is difficult to say. We cannot assume that a young male and a young female never mate together, for if we consider the proportion of young birds to old, we can see that cases must frequently arise in which a pair are compelled to build a nest and rear young antecedent to experience. In some of the cases which I have from time to time studied, there is a strong probability that the actors have been performing for the first time; and, if so, they have taken their part in this complex piece of machinery as skilfully as the adults. It is true that we could place their whole behaviour on a level with our own; we could discern a motive in their supplying one individual more than another with food, could regard the removal of the faeces as an act of conscious deliberation, could indeed see all their actions in the highest light possible and thus attribute to them reasoning powers similar to our own; but of what use would such a method be? Conclusions thus reached would retard rather than facilitate our knowledge of their subjective states, and it might truthfully be said that they would never even enter the domain of science.

I have in the case of this species also carried out a series

of experiments by placing a leaf in the nest in order to see in what manner the parents would adapt themselves to the unusual conditions thus presented; whether, as in the case of the Whitethroat, they would treat it as if it were faeces ejected by the young, or whether they would recognise the nature of the obstruction. On the whole, there is little difference between the behaviour of the two species. I have never seen a Reed Warbler actually swallow a leaf, but its efforts to do so are equally as pronounced as those of the Whitethroat, and its failure may be due to physical reasons. The leaf is picked up and held in the bill, while at the same time the movements necessary for swallowing are performed; it is then perhaps dropped, but again picked up and finally carried away. When a number of leaves are placed in the nest at the same time, those that slip in between the young and are pushed to the bottom are allowed to remain. If a leaf of the same size as the interior of the nest is placed over the young, thus completely hiding them, the female on her return takes little notice. There is a slight examination and slight bewilderment, but nothing more; then she settles down upon the nest and attempts to brood in the usual manner. However, the discomfort, and perhaps the feeling that her legs and feet are not in their proper position and her feathers not satisfactorily covering her young seem to make her restless, and in her struggles to put matters right the leaf is soon pushed over the edge.

Incidents sometimes occur of so little importance in themselves that they may almost seem to savour of triviality, but whenever they are in the nature of a check to the normal routine of activities, whenever, that is to say, adaptation to unusual circumstances is required, then such incidents in themselves may be said to constitute an experiment, the result of which is of relatively equal value in enabling us to judge of the mentality of the actor as the result of an experiment planned and carried out by the human mind. I can recall two such incidents, both of which occurred while food was

being carried to the young. It is not an uncommon habit amongst many species, and it may occur at any moment after mating has taken place, for the male to feed the female ; and so it happened that while a pair were carrying food to their young and were within a short distance of one another, the male clinging to a reed stretched out his neck to the female, who was also clinging to a reed but facing him, and attempted to feed her in the usual way. The attitude of the female was characteristic ; she uttered her quiet subdued note while at the same time fluttering her wings after the manner of a young bird. The male also uttered a call-note. Both of them had their bills full of insects at the time, and it is quite clear that the female did not require the food, otherwise she would have swallowed the insects she was carrying ; and it is also clear that if she had opened her bill to receive food from her mate much of that which she was carrying would have fallen out.

The second incident was even more trifling. One of the birds with its bill full of insects attempted to peck at something which was apparently irritating its leg ; this of course it was unable to do owing to the large number of insects in its bill, and consequently it seemed completely puzzled, again and again bending its head forwards, and, while examining its leg, moving its head as if on the point of pecking, but its mental capacity did not seem equal to the occasion.

After the young are a few days old, and as they become more active, they respond more spontaneously to the approach of their parents. But they do not seem able to distinguish their own parents from other individuals of the same species. Even a gentle swaying of the reeds is sometimes sufficient to cause them to stretch up their necks and open their gapes, so that in a strong wind when the reeds are blown this way and that, they seem to be unaware of the approach of a parent until it is actually on the edge of the nest itself. The noise of the wind no doubt prevents them from hearing the call-note which they recognise and respond to.

It may be remembered that some of the young are stronger than others, and that one will often make a short excursion into the reed bed a day or so before the nest is finally deserted, eventually returning. Upon a young wanderer thus returning I have seen the remaining birds in the nest just as excited and expectant as if it were a parent arriving with food, stretching out their necks and not realising the position even when the wanderer was elbowing its way amongst them. Whether the young after having deserted the nest return in the evening to roost I cannot say. For a while they keep close to one another in the reeds, but they soon become scattered, and when a reed bed is inhabited by a number of pairs one can hear the plaintive call-note of the young proceeding from every direction. At this age they are difficult to find and difficult to catch, for, though unable to fly, they travel quickly by hopping from one reed-stem to another. In wet weather, or when the dew has been exceptionally heavy, which in July is often the case, their appearance is most pitiable, as their feathers are bedraggled with the water which collects on the reeds in such a quantity, especially at the junction of the leaf to the stem. I once, after some delay owing to the difficulty in locating the sound, found a young one which could only have left the nest very recently, perched upon a large branch of an alder in such a position that it was impossible to see it when standing directly underneath. The weather at the time was wet and the condition of the little creature was most miserable. It had but few feathers on its body and they were so bedraggled as to be of little use. How, in such a plight, it climbed so high from the ground it is difficult to understand. It is probable that the young are more hardy than those of many other species, for they may be found in a similar condition more or less every morning, and although the feathers dry very rapidly in the sun, yet it must require an exceptionally robust constitution to withstand so constant a drenching; possibly many do succumb to cold and exposure. How the parents feed their offspring when thus scattered, and



MALE REED WARBLER

ATTITUDE ASSUMED DURING THE
PERIOD OF SEXUAL ACTIVITY

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SWAN, ELECTRIC PEN, NEW YORK.

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whether they are able to distinguish the call-note of their own from that of other young, it is difficult to say. The same factor which we discussed earlier no doubt guides them in regard to feeding in rotation ; those that are the more hungry are possibly the more persistent in uttering their call-note and do so the more loudly. Owing to the conditions under which they are born and reared it is probable that there is a very considerable mortality amongst them, any tendency to weakness being rigorously eliminated. The young of other species of the same genus are comparatively secure even upon the ground, and can, indeed, often be found after they have left the nest hidden amongst the undergrowth. But the young Reed Warblers must be prepared to take their place in the struggle for existence immediately they leave the nest ; any weakness that would prevent them from indefinitely clinging to the reeds until capable of considerable powers of flight would be fatal and could only result in their destruction ; and to meet this difficulty it probably is the case that they remain in the nest longer than those of some other closely allied species, since any tendency to leave it too early would be held in check. The weakling would neither be able to withstand the cold, wet weather, nor could it keep up with its parents or even attract their attention when desirous of food. In fact, the struggle for existence must, in their case, be exceedingly severe.

Throughout the whole of June and July periodical outbursts of excitement occur amongst the different individuals inhabiting the reed bed, such outbursts being apparently not confined to one sex only, although in most instances the males are probably the sole actors. To determine what are the causes which lead up to these activities is difficult ; it is not even possible to decide whether the participants are in earnest and the struggles genuine, or whether their behaviour is an expression of exuberance of energy. Play forms an important part in the life-history of many mammals. The rabbit, the hare, or the fox can be seen practising for the

more serious side of life, each in its own particular way; and there is no reason to suppose that this trait is absent from bird life. But it is by no means probable that the petty struggles, rapid pursuits, or harsh scoldings, which are of common occurrence in the life of this species, can all be referred to this cause, or that they have one and the same origin. On the one hand we have scolding parties, very similar to those we find in the life-history of the Sedge Warbler. As many as six individuals, apparently belonging to both sexes, collect in a small area, some at the tops of the reeds and some at the bottom, and produce a considerable commotion by uttering their harsh scolding note. On the other we frequently find a number of individuals pursuing one another, darting in and out of the reeds, momentarily appearing as they fly above the tops, but rapidly disappearing again from view, pecking at and fluttering with each other in the air or amongst the reeds when the unusual shaking of the stems discloses their exact position; and yet again we find two or more close together bursting into song and uttering their notes more hurriedly and more excitedly than under ordinary conditions.

As already mentioned, the date of arrival of different individuals varies considerably. The case may be remembered of the two males which appeared within a few days of one another; the one secured a mate only upon the day on which its neighbour's young were preparing to leave the nest. Thus it will be seen that in the same reed bed and at the same time, reproduction may exist in all its different stages. In one territory a male may be mating, in another a pair may be busy with incubation, while in another the young may be on the point of leaving the nest. So that we have in this fact a possible explanation of much of the excitable behaviour of different individuals; for the question of territory is not comparatively absent, as it would be if the young of all the different pairs were ready to leave the nest, but, rather, a prominent cause of strife even up to

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the middle of July. This, I think, may often be an explanation of the quarrelling ; but without further observation it would be unwise to speculate upon the cause of the gathering together of different individuals, of the spontaneous outburst of song, and of the pursuits, which possibly are not in earnest.

Quarrels between this species and Sedge Warblers are not uncommon, sometimes one being the aggressor, sometimes the other. They dart at one another with the usual clicking of bills ; and of the two the Reed Warbler seems to be the stronger. But I have seen a male Sedge Warbler interfere in a most unjustifiable manner. This particular male owned a territory in some alders adjoining the reeds, and, as is their wont, favoured one particular tree, from which he constantly performed the aerial flight and song peculiar to the species. Now a pair of Reed Warblers were located some little distance away, and, as if for pure enjoyment, he would suddenly and rapidly dart at one or other of them, pursuing it amongst the reeds and thus causing considerable commotion. There was no obvious reason for such behaviour, unless we regard it solely as practice for the more serious side of its existence, that is to say, the necessary defence, which might at any moment arise, of its territory.

Few birds sing under smaller provocation. Even a stone thrown into the reeds is often sufficient, and the advent of a Jay (*Garrulus glandarius*), or a Magpie (*Pica rustica*) will sometimes produce a spontaneous outburst in which the majority of the males take part. The spontaneity with which these outbursts occur is very striking. One, or perhaps two, males may be leisurely singing, when suddenly, and often for no apparent reason, all the males burst into their hurried excitable song for a few moments only, and then again lapse into silence. The song in which the female occasionally indulges is peculiar, and differs in this respect from that of all other members of the genus, excepting the Great Reed Warbler (*Acrocephalus turdoides*), that it does not flow evenly from

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the throat of the performer, but is uttered in a jerky manner, giving one the impression of a number of short sentences with a full-stop at the end of each one, and of considerable effort in commencing each new sentence. Notwithstanding this peculiarity, their vocal powers may be said to have reached a very high degree of development. To my mind their song possesses an element of cheerfulness, due to some extent, no doubt, to pleasant associations, and the tone possesses a peculiar metallic ring which is not present in a similar degree in the song of other birds with which I am acquainted. When the males first arrive their song is persistent, but after incubation has commenced it is not uttered so frequently, and ultimately it is to a large extent limited to the spasmodic outbursts referred to. In addition to the song there are numerous call notes, some of which are very similar to and difficult to distinguish from those of the Sedge Warbler. It is possible to distinguish three distinct calls; the call-note proper used frequently by both sexes during the mating period, and also when the young are being attended to; the scolding note peculiar to the assemblies; and a harsh note uttered two or three times in succession, apparently as an expression of anger or annoyance, since it is usually the forerunner of much fluttering and clicking of bills. But the most interesting part of their vocal development is undoubtedly the power of imitation, which, when first heard, seems to equal that of the Blackcap or Marsh Warbler. In reality, however, the bird is not so finished an imitator as these other two species; for whereas the Blackcap will produce part or whole of the song of another species in so perfect a manner as to deceive the human ear, the Reed Warbler does not seem to be capable of doing so. Its imitative faculty is generally limited to reproducing the call notes and cries of various species inhabiting the same neighbourhood, but some are undoubtedly produced from memory. I have heard a male, inhabiting some reeds surrounding an inland sheet of water, imitating the cry of the

Redshank (*Totanus calidris*). The alarm-note of the Blackbird is often well imitated, and the call-note of a Pied Wagtail (*Motacilla lugubris*) fluttering out of the reeds, or of a King-fisher (*Alcedo ispida*) flying above, is sometimes well reproduced. The cries of the different Terns, where a colony happens to be breeding in proximity to a reed bed, will often be incorporated with the song, and I have also heard perfect imitations of a call-note of the Blue Tit, Chaffinch, Icterine Warbler (*Hypolais icterina*), Sedge Warbler and Willow Warbler. But in judging of the power of imitation it is necessary to bear in mind the possibility of some of the notes, which are apparently perfect copies of those of another species, being in reality a natural part of the vocal powers of the imitator. For instance, I remember hearing a Blackbird introduce into its song throughout the breeding season the cry of the Curlew (*Numenius arquata*) in a very perfect manner. Possibly it may have heard a Curlew, but in the district in which it was singing it is scarcely probable that it had done so, for that species, with the exception of an individual occasionally passing over at a considerable height, is unknown there. At the time I did not believe that the imitation, perfect as it was, was genuine, but rather part of the true song slightly altered, and later I was confirmed in this opinion upon finding that only a slight alteration is required to produce such a result. There are some imitations which we need not hesitate to declare to be imitations pure and simple. When a bird interrupts its true song, and for a few moments introduces that of another, differing in combination and possibly in tone, we can point to it with some certainty as an imitation. On the other hand there may be a perfect resemblance in the song of two species which we can be equally certain has no foundation in the imitative faculty. It is only with difficulty that the true song of the Icterine Warbler can be distinguished from that of the Marsh Warbler, yet no one could say that one is an imitation, although it may be a perfect representation, of the other. Both songs

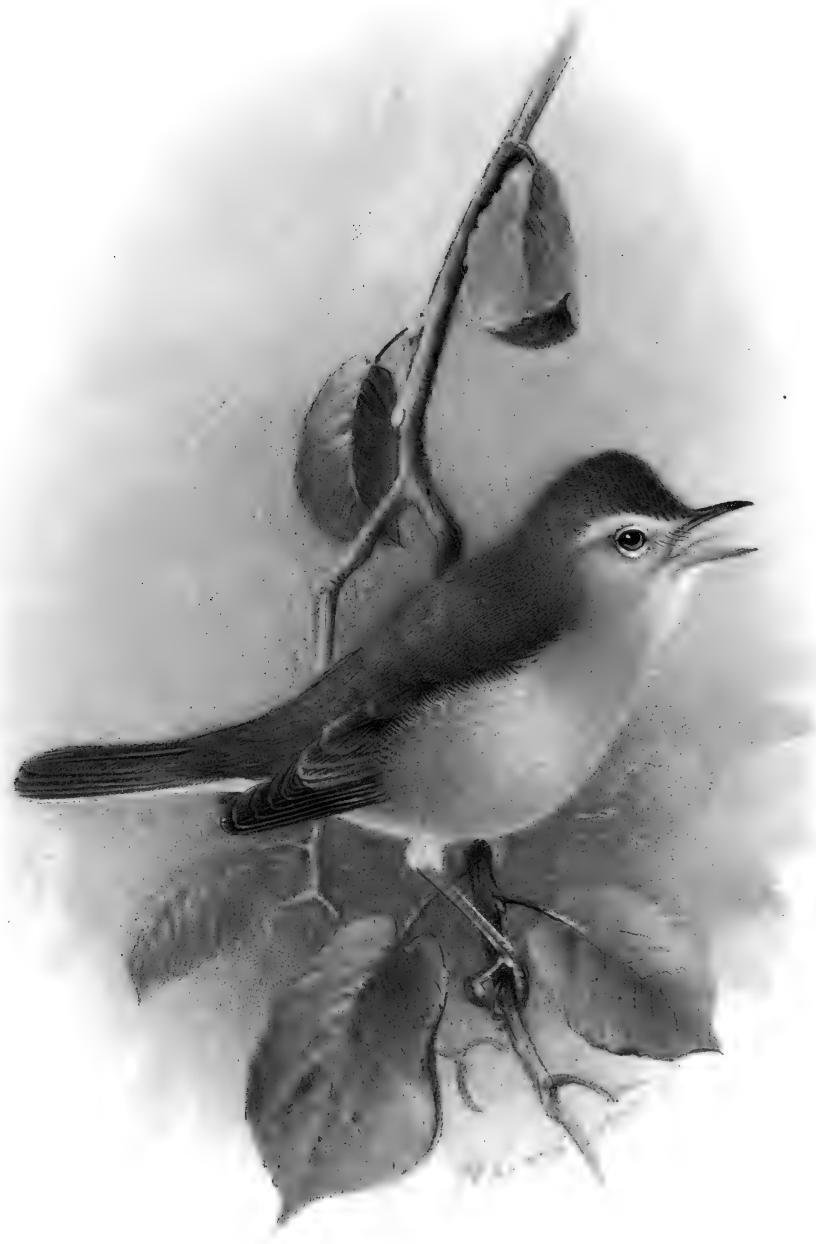
are complete in themselves, and both birds are equally good imitators of the songs of other species. Between these two extremes there are a large number of notes uttered by different species which are very similar, and may or may not be imitations. I refer more especially to the call-notes, which, being as a rule single notes, would the more easily be imitated, and at the same time the more likely to be a natural production. But when we consider the extraordinary number of songs, call-notes, and combinations of sounds, produced by bird life in general, we ought surely to be astonished, not that we can occasionally detect a similar note in two different species, but that we cannot more frequently do so.

In the song of different individuals there is little variation, nothing in fact to show that it reaches a higher degree of perfection year by year, excepting perhaps that a greater number of imitations may be remembered and reproduced.

Their food consists principally of insects, *Chironomidæ* and *Limnobiidæ* being devoured in large quantities. But *Aphides* may be said to form their staple diet, and these they find clustering on the leaves of the reeds and on the branches, twigs, and buds of the alders and willows surrounding the reed bed. It is always a difficulty to determine exactly what the insects are which are being taken and supplied to the young, since their digestive powers act so rapidly. Even dissection of a young bird immediately after the parent has supplied it with food is of little use, the insects by that time being reduced to a pulp by the digestive fluid, and consequently beyond recognition. This result is not due to their being supplied with regurgitated food, for one can see the insects being caught, carried, and delivered even in a living condition into the throats of the young. For the purpose of identifying the insects, I have from time to time made a number of experiments, but hitherto with little success. Small pieces of cotton-wool placed in the throat and secured with a fine thread prevented some of them from being swallowed, if removed immediately the

REED WARBLER

parent had finished its task. But it was by no means satisfactory, as the wool caused irritation in the throat, and the young bird consequently made repeated efforts to swallow it. The insects supplied are as a rule crushed in a lump by the bill of a parent, but they are not always dead, and occasionally one will make good its escape when too many have been placed in the throat at one time.



MELODIOUS WARBLER.

Hypolais polyglotta, Dresser, *Birds of Europe*, vol. ii, pl. 80 (adult male), pp. 517-519, 1874; Saunders, *Manual of British Birds*, 2nd Ed., pp. 77-78 (woodcut), 1897.

German, *Kurzflügeliger Gartenspötter*; Arabian, *Belbél*; French, *Bec-fin ictérine*; Italian, *Canapino*; Portuguese, *Folosa*; Spanish, *Almendrita de verano*; Hungarian, *Déli füzike*.

DESCRIPTION OF THE PLUMAGE.

Adult Male in Spring.—The upper parts are uniform olive green washed with a light brownish colour, the rump being a more distinct olive. The wing and tail-feathers are brown, the bastard wing, primaries and their coverts, being narrowly edged with light buff, whereas the median coverts, secondaries and their coverts, are broadly margined with that colour. The least wing-coverts are the same colour as the back, and the tail-feathers are narrowly edged with light buff. The lores and the distinct superciliary stripe are, like all the under parts, a bright yellowish colour. Axillaries and under wing-coverts are light buffish yellow, the under parts of the wing and tail lavender brown, and the shafts of the feathers whitish. The bill is a brownish horn colour, the lower mandible being buffish yellow at the base, and the mouth orange red. The iris is dark brown, and the feet horn brown.

The female resembles the male.

Adult in Autumn.—The upper parts are slightly more greyish buff, and the lower a brighter yellow. The autumn plumage of the young is similar to that of the adults.

Nestling.—The upper parts are almost buffish grey with a slight trace of olive, the under parts being ochre yellow.

GEOGRAPHICAL DISTRIBUTION.

This species seems to visit the **South Coast** only of **England**. There are two records from Sussex and one from Cornwall, but the southern part of Devonshire appears to have been repeatedly visited. In the remainder of the British Islands there has been only one occurrence, a specimen having been obtained at the Old Head Lighthouse, Kinsale, co. Cork, in September. On the **Continent** the bird is principally an inhabitant of the south-western parts. One specimen has been obtained in **Heligoland**. **Belgium** is occasionally visited, so is the Valley of Metz in **Germany**; and there is one record from **Austria**, one from Lenkoran in **Trans-Caucasia**, and it has been obtained in the south-western part of **Hungary**. In **France** it does not breed north of the Seine, but in the centre, west, and south-west it is generally distributed and common; while in the east it is found in the provinces of Cote d'Or, Savoie, Haute-Savoie and Jura. Throughout **Spain** and **Portugal** it appears to be common. In **Africa** it is plentiful in **Algeria** and **Tunis**, and it inhabits **Morocco**, the country between Morocco and the River Senegal, and the **Gold Coast Colony**; but in **Egypt** its occurrence seems doubtful.

In winter it appears to resort principally to **South** and **West Africa**.

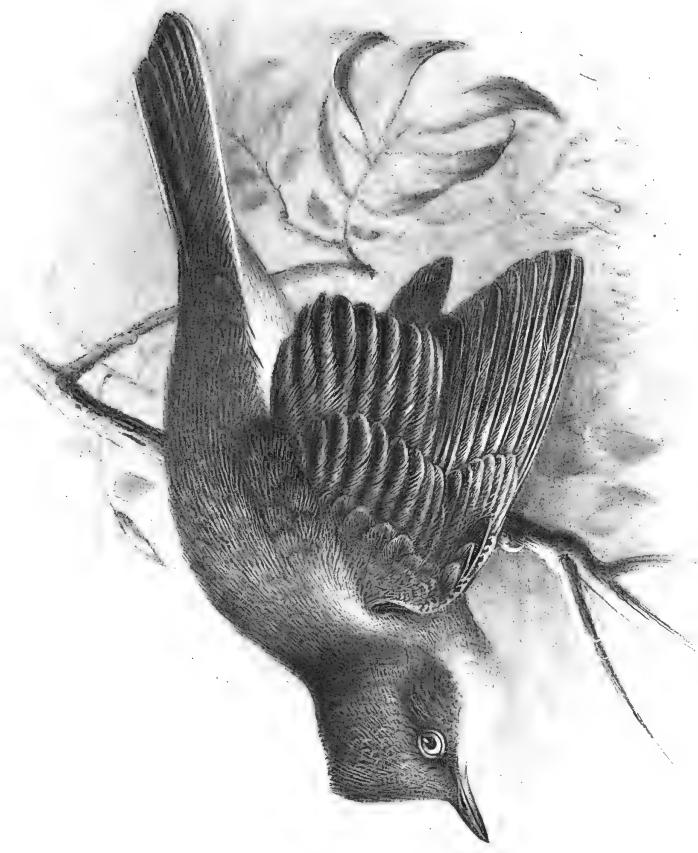




UNFAIRRED MALE WHITETHROAT
WATCHING TWO FEMALES FIGHTING
IN HIS TERRITORY

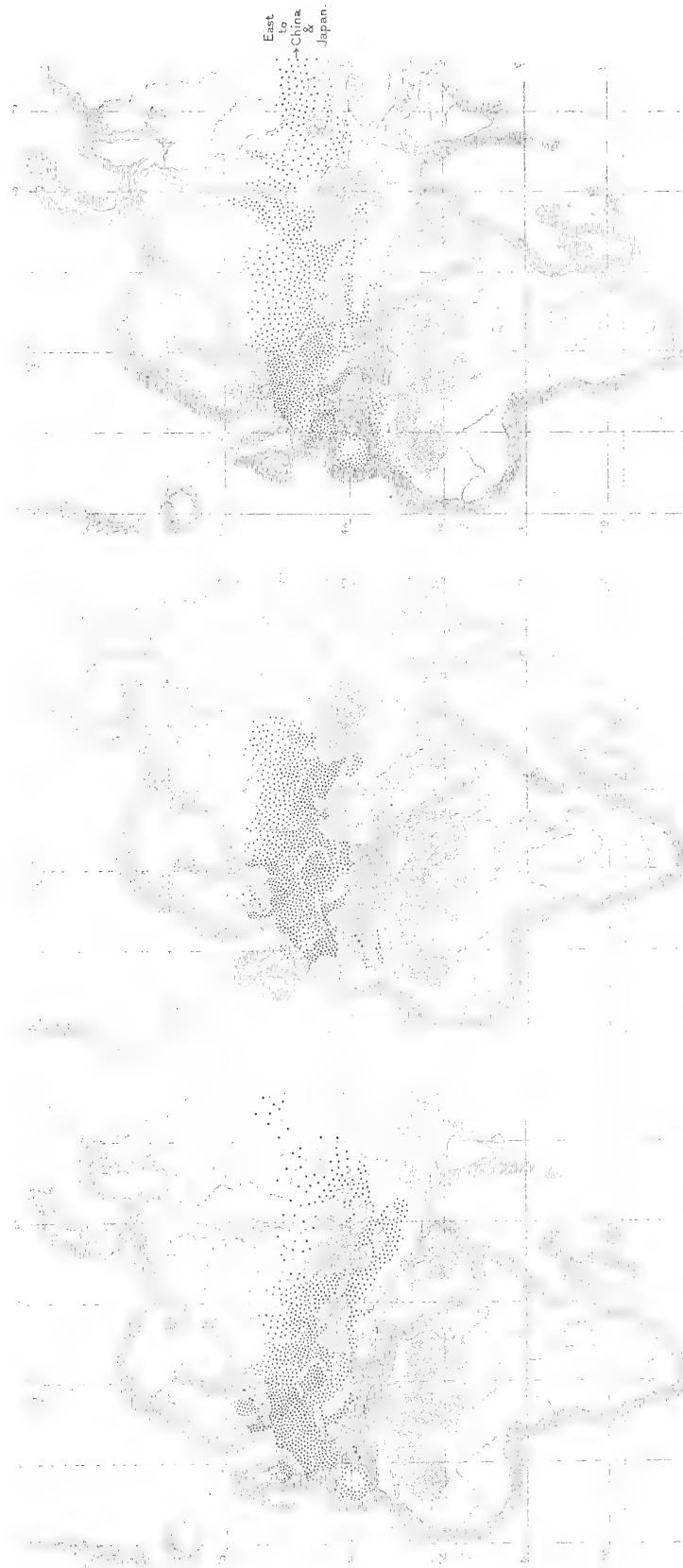
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FEMALE, WHITE-THROAT
ATTITUDE ASSUMED WHEN THE
NEST IS APPROACHED





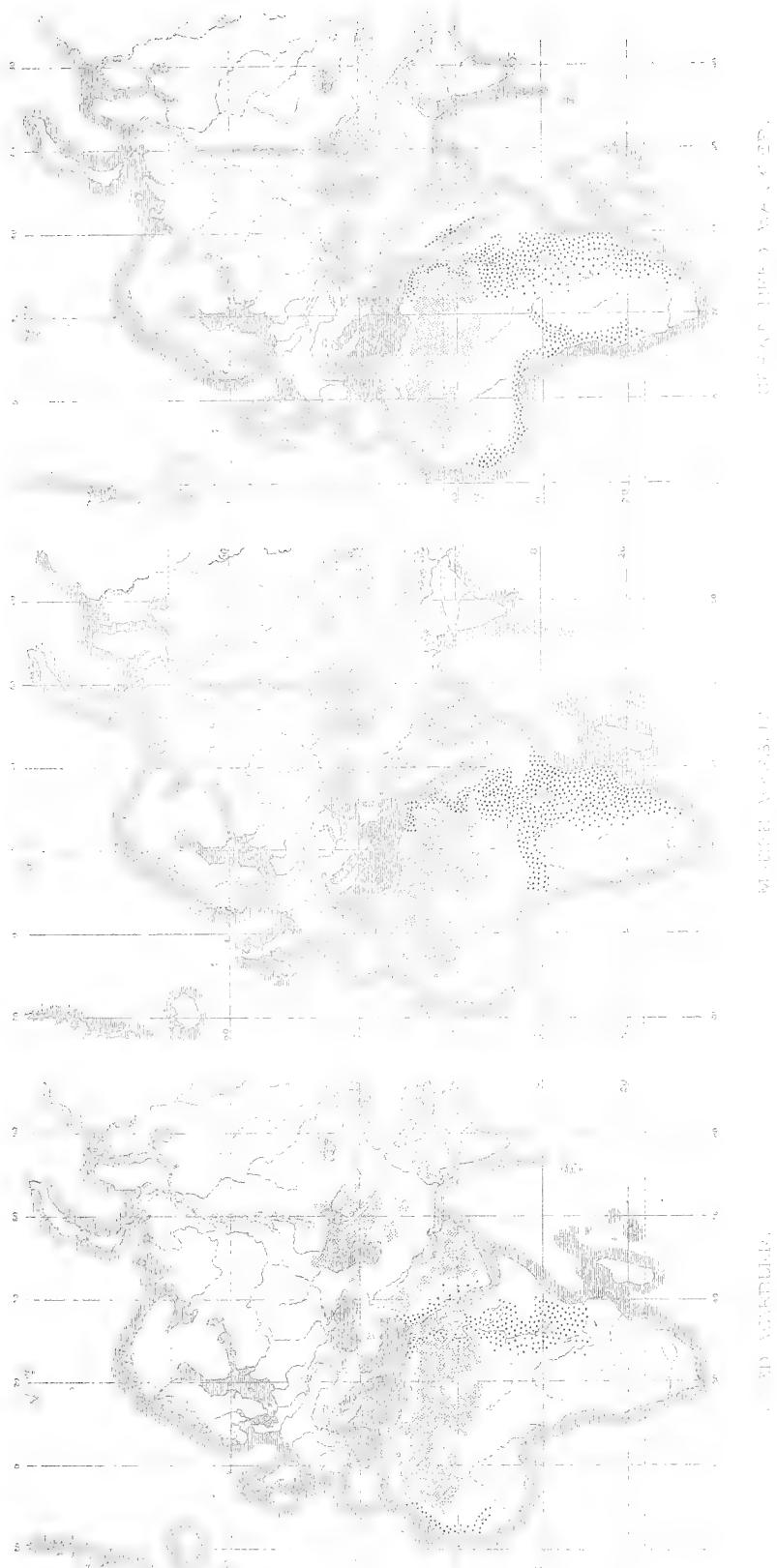
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BATHYGRAPHICAL DISTRIBUTION DURING SUMMER

PUBLISHED BY R. H. SPURGEON

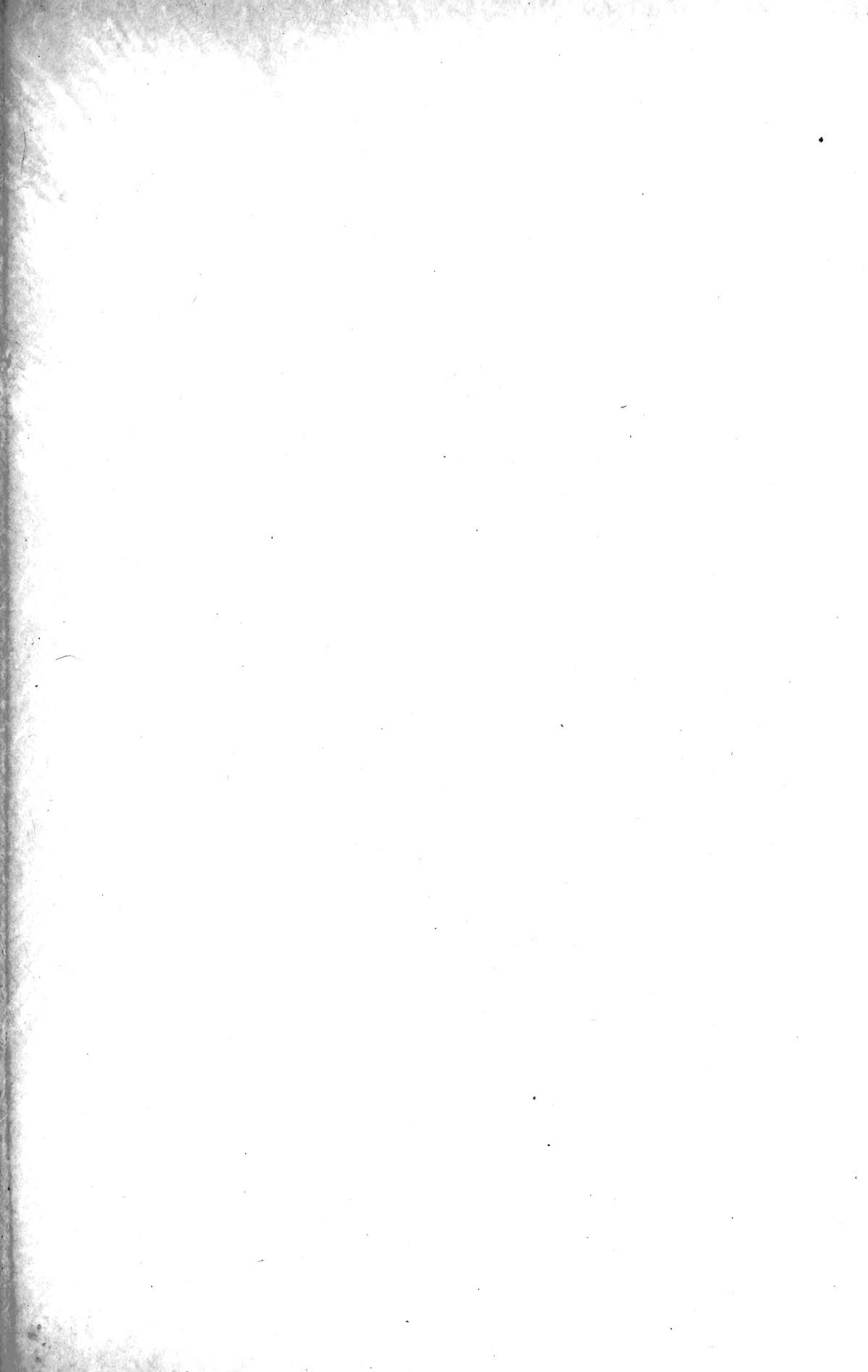
FIG. 34. BATHYGRAPHICAL DISTRIBUTION DURING SUMMER

BALE & LAMBERTSON, 1951



Geographical distribution of seals in the Arctic
 (modified from: 1. B. B. Hansen
 2. G. L. Shaffer
 3. V. V. Kondratenko
 4. V. V. Kondratenko, 1972)







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